

THE NEURO-ETHOLOGY OF MOUSE AGONISTIC BEHAVIOUR

INAUGURAL-DISSERTATION

zur
Erlangung der Philosophischen Doktorwürde
vorgelegt der
PHILOSOPHISCHEN FAKULTÄT II
der
UNIVERSITÄT ZÜRICH

von
STEPHAN STRASSER
aus Nussbaumen TG und Winterthur ZH

Ausgeführt bei Dr. A.K. Dixon, am
Sandoz Forschungsinstitut in Bern

Begutachtet von den Herren
Dr. A. K. Dixon Sandoz Forschungsinstitut Bern AG
Prof. Dr. R. Wehner
Zoologisches Institut der Universität Zürich
Dr. G. Ehret Abteilung für Biologie der Universität Konstanz

Zürich 1987

Zbinden Druck und Verlag AG
Basel

THE NEURO-ETHOLOGY OF MOUSE AGONISTIC BEHAVIOUR

INAUGURAL-DISSERTATION

zur
Erlangung der Philosophischen Doktorwürde
vorgelegt der
PHILOSOPHISCHEN FAKULTÄT II
der
UNIVERSITÄT ZÜRICH

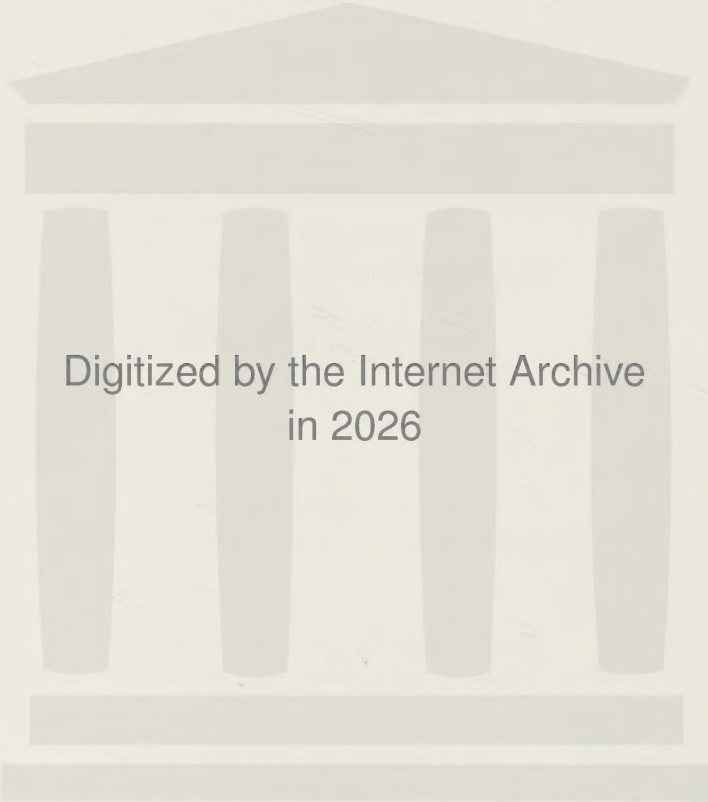
von
STEPHAN STRASSER
aus Nussbaumen TG und Winterthur ZH

Ausgeführt bei Dr. A.K. Dixon, am
Sandoz Forschungsinstitut in Bern

Begutachtet von den Herren
Dr. A. K. Dixon Sandoz Forschungsinstitut Bern AG
Prof. Dr. R. Wehner
Zoologisches Institut der Universität Zürich
Dr. G. Ehret Abteilung für Biologie der Universität Konstanz

Zürich 1987

Zbinden Druck und Verlag AG
Basel



Digitized by the Internet Archive
in 2026

To my parents

I would like to express my thankfulness to :

Dr. A.K. Dixon for his help and advice throughout the direction of this work and for the many invaluable discussions; and Prof. Dr. R. Wehner for advocating my work at the Faculty of Philosophy at the University of Zurich.

Dr. H. Kuehne, Mr. M. Schaer, Mr. Aeberhard, Mr. W. Stauffer and Mr. D. Eicher for the help with the data analysis. Miss C. Huber for methodological advice. Mr. A. Reber for animal care and Mr. R. Aeberhard for supplying me with wild mice. Mr. F. Iseli for the construction of the apparatus and appliances. Miss B. Stampbach for help and instruction on brain lesions and subsequent preparation of these brains; and Miss F. Meier for histological analysis of the brain preparations. Mr. H. Stocker, Mr. J. Marti and Mr. D. Huebener for graphics and photographs. Dr. S. Qureshi and his co-workers, Miss B. Greiner and Mr. P. Stirnimann for preparation and histological analysis of ZnSO_4 -treated nasal cavities. Dr. G. Ehret for performing the sonagrams of mouse rustling noises at the University of Konstanz, FRG. Dr. M. Lehrer, and Dr. H.P. Kaesermann for reading the manuscript. Finally, Miss U. Schmid, for patience and sympathy.

Dr. F. Kunz and Dr. P.L. Herrling for their personal engagement and interest in this work.

This thesis was carried out at the "Sandoz Research Institute Berne, Ltd." and was supported by a grant awarded by SANDOZ Ltd., Basle.

TABLE OF CONTENTS

I. INTRODUCTION	1
II. ANIMALS AND METHODS	7
1. Animals	7
2. Behavioural analysis	7
2. 1. Setup for enclosure experiments	7
2. 1. 1. Evaluation of territorial behaviour	10
2. 2. Setup for cage experiments	11
2. 2. 1. Evaluation of aggressive behaviour in cages	13
3. Deprivation techniques	15
3. 1. Olfactory deprivation	15
3. 2. Acoustic deprivation	16
3. 3. Visual deprivation	16
3. 4. Vibrissal deprivation	17
4. Lesion technique	17
5. Histology	18
5. 1. Analysis of brain lesions	18
5. 2. Analysis of olfactory mucosa	19
6. Sonographic recordings	19
7. Preparational and statistical data analysis	19
7. 1. Smoothing crude data	19
7. 2. Wilcoxon-test	20
7. 3. Mann-Whitney U-test	20
7. 4. t-Test	20
7. 5. X^2 -Test	20
III. RESULTS	21
Part A: Analysis of agonistic behaviour in territories	21
1. The behavioural structure of territorial defense	21
2. Effects of sensory deprivation on territorial defense behaviour	23
2. 1. Acoustic deprivation	24
2. 2. Visual deprivation	25

2. 3. Combined acoustic and visual deprivation	26
3. Sensory-physiological characterization of some behavioural phases associated with territorial defense	27
3. 1. Attending behaviour	27
3. 2. Tracking behaviour	29
3. 2. 1. Acoustic tracking	29
3. 2. 1. 1. Monaural tracking	36
3. 2. 2. Visual tracking	39
3. 3. Attacking	40
4. Lesion experiments	42
4. 1. Lesions placed in the Superior Colliculus	43
4. 2. Control lesions	45
Part B: Analysis of agonistic behaviour in cages	47
1. The development of cage aggressive behaviour	47
2. Time analysis of cage aggressive behaviour	48
3. The effects of sensory deprivation on cage aggressive behaviour (CAB)	50
3. 1. Effects of olfactory deprivation on CAB	50
3. 1. 1. Restoration of agonistic behaviour after olfactory deprivation	51
3. 1. 2. The histological analysis of the effects induced by ZnSO ₄	53
3. 2. Effects of acoustic deprivation on CAB	54
3. 3. Effects of visual deprivation on CAB	55
3. 4. Effects of vibrissal deprivation on CAB	57
3. 5. Effects of combined visual and vibrissal deprivation on CAB	58

IV. DISCUSSION	61
1. The structure of mouse agonistic behaviour	61
2. The sensory control of agonistic behaviour and its phases	63
2. 1. Motivation for aggressive behaviour (olfaction)	64
2. 1. 1. Implications for the olfactory sense	67
2. 2. Visually guided behaviour	68

2. 2. 1. Implications for the visual sense	71
2. 3. Acoustically guided behaviour	73
2. 3. 1. Implications for the acoustic sense	74
2. 4. Tactile control of agonistic behaviour	77
2. 4. 1. Implications for the tactile sense	79
3. Sensorimotor-interfacing and tracking	79
4. Two acoustic-systems hypothesis	82
5. Methodological issues	83
5. 1. Olfactory deprivation (ZnSO_4 -solution)	83
5. 2. Visual deprivation (contact lenses)	85
5. 3. Acoustic deprivation (ear-plugs)	86
 V. EPILOGUE	 88
 VI. SUMMARY	 90
 VII. APPENDIX	 93
A. Cage aggressive behaviour (raw-data)	93
B. Histological analysis of lesions	110
 VIII. LITERATURE	 113

Of all laboratory animals probably none has contributed more to the advancement of knowledge than the common mouse (SNELL, 1941)

I. INTRODUCTION

To obtain a picture of the outside world and to appropriately guide actions in it, animals must - by means of their specific sensory and neural equipment - select, read and interpret the information present in the environment in various ways and with various degrees of sophistication, according to their habitat and the complexity of their behaviour.

The task to unravel just how this is done, may be tackled using many different approaches. Perhaps the most fundamental distinction in recent years has been made between those who remained at the behavioural level and those, who sought answers in physiological terms. To study behaviour in its own right (i.e. to use an ethological approach) would be to treat an animal as "black box", trying to understand how behavioural output is depending on sensorial input without being concerned with the exact nature of the

intervening mechanisms. This approach was favoured e.g. by LORENZ, TINBERGEN and von FRISCH, but other researchers, e.g. von HOLST, AUTRUM, ROEDER went further and attempted to analyse behaviour in terms of neural circuitry as a necessary link between sense organs and muscles to produce certain actions. In the last decades both approaches have reached a high degree of sophistication and a number of new techniques have been introduced, to study behaviour in ethological physiological and neuro-anatomical etc. terms. From this work, a new approach has evolved integrating behaviour, physiology and neural events and, since about the mid 1960's has become known as **neuroethology**. Due to its interdisciplinary character, there has been a great increase in neuroethological literature in the last two decades (for reviews see e.g. ROEDER, 1963; GUTHRIE, 1980; HUBER and MARKL,

1983; EWERT, CAPRANICA and INGLE, 1983; CAMHI, 1984). Although many different opinions exist on how to define neuroethology (see e.g. EWERT 1976;) HUBER, 1983; HOYLE, 1984), the common aim is generally recognized as being to link behaviour and physiology in a functional manner, i.e. how do animals (and man ultimately) succeed in producing behaviour adapted to a certain "umwelt". Concerning vertebrate neuroethology, there has been a general emphasis on comparative physiology (BULLOCK, 1983) using non-mammalian as well as mammalian species and some well known case studies are e.g. prey catching and predator avoidance in toads (EWERT, 1976), echolocation behaviour in bats (GRIFFIN, et.al., 1960) or visuomotor behaviour in rodents (FINLAY and SENGELAUB, 1981; INGLE, 1981a).

The aim of this thesis is to apply a neuroethological approach to the study of mouse aggressive behaviour, the latter being a substrate for many ethological, physiological as well as pharmacological studies.

The mouse has always been in particular favour with many

scientists and thus is one of the best investigated research animals and many investigations have been performed related to the topic of agonistic behaviour in mice. Thus, it has been shown, that the housemouse in its natural habitat is territorial, either when living commensal with man (ANDERSON, 1961; CROWCROFT, 1955) or under feral conditions (feral = not associated with man) (BERRY, 1968), and MACKINTOSH (1978) reports an example of a social interaction between two males seemingly fighting at their territorial boundary. Territoriality can also be established in enclosures (CROWCROFT and ROWE, 1963; REIMER and PETRAS, 1967; MACKINTOSH, 1970), where a minority of males (i.e. the territorial animals) dominate a number of cohabiting males (subordinates), that are non-territorial although they may occasionally assist in territorial defense against foreign intruders. When held in groups in laboratory cages, mice no longer establish territories but form social hierarchies (UHRICH, 1938; SCOTT and FREDERICSON, 1951; POOLE and MORGAN, 1973), the social structure and its

stability depending on the number of individuals and the space available (POOLE and MORGAN, 1976). When isolated in cages, male mice are seen to develop a behavioural "isolation syndrome" (VALZELLI, 1973; BRAIN, 1974), the most distinctive feature of it being an obvious increase in aggressivity (VALZELLI, 1969; CAIRNS et.al., 1984). The above findings testify to the ease with which mice can be persuaded to behave aggressively, which was one of the reasons to select mouse aggressive behaviour as a model to perform the subsequent study.

The capacities of the various sensory modalities have been the second widely treated topic but have been investigated mainly for their physiological aspects, and in some cases (i.e. olfaction and audition) in considerable depth. In mice like in most mammals, five afferent systems which may contribute to "olfactory sensation" are acknowledged (e.g. BREIPOHL et.al., 1985) the two most important pathways of chemosensory access to the central nervous system being 1. the primary olfactory system, arising at the olfactory epithelium in the nasal cavity and projecting

through the main olfactory system, 2. the vomeronasal system, arising at the level of the vomeronasal organ and projecting through the accessory olfactory system (SCALIA and WINANS, 1975; TAKAGI, 1981). Effects induced by various olfactants and especially mouse urine have repeatedly been shown and are commonly divided into a) priming and b) releasing effects. Priming effects i.e. induction of physiological changes such as pregnancy block (BRUCE-effect, 1959), lengthening of oestrous cycle (LEE-BOOT-effect, 1955) and shortening and synchronization of oestrous cycle (WHITTEN-effect, 1956) are supposedly mediated by pathway 2 (SAITO and MOLTZ, 1986), whereas behavioural changes such as induction of sexual (DIXON and MACKINTOSH, 1971) or agonistic (ROPARTZ, 1968b; MUGFORD and NOWELL, 1970) behaviour are probably associated with pathway 1. Since the mouse acoustic system is considered as being representative for mammals there has also been great interest in the auditory biology of the mouse. EHRET (1974, 1976) has supplied an auditory action spectrum for the mouse. Most of

the studies however concentrated on anatomy (e.g. SAUNDERS and GARFINKLE, 1983; EHRET, 1983; WILLARD and RYUGO, 1983) and neurophysiology, where knowledge on structure and function of neural centres in the auditory pathway (i.e. brainstem auditory nuclei or Inferior Colliculus) is now reasonably detailed (for a review see e.g. WILLOT, 1983). Auditory guided natural behaviour likewise has received little attention or was restricted to aspects of sound communication among adults (e.g. SALES and PYE, 1974; WHITNEY and NYBY, 1983) or between parents and offspring (e.g. NOIROT, 1972; HAACK et.al., 1983). However, it has not been shown if and to what extent mice attend to acoustic signals under natural or semi-natural conditions. In contrast to audition many rodent species - except the mouse - have been used for studies of vision, thus, little is known about the role of vision in the mouse. It has been shown that mice are capable of solving quite difficult pattern discrimination tasks, when allowed to approach stimuli close enough (BOXBERGER, 1953), and MACKINTOSH (1973) has demonstrated that in

large enclosures, male mice appear to use visual cues for the detection of territorial boundaries.

Despite this enormous wealth of knowledge on the mouse, gaps still exist between descriptive behavioural analysis and the underlying sensory and neural correlates. It is here, that a neuroethological approach has much to offer. There have been attempts to relate sensory input to certain behavioural actions, using deprivation or lesion techniques. Thus it has been demonstrated that olfactory bulbectomy (ROPARTZ, 1968b) as well as olfactory epithelial destruction using $ZnSO_4$ (BRAIN et.al., 1982a) abolish aggressive behaviour. BEACH (1942) found that blind mice apparently fought and mated without difficulty and KALKOWSKI (1968b) considered visual cues as not essential mediators of social interactions during encounters where mice were deprived of physical contact. KATZ (1976) and BRAIN et.al. (1982b) by removing the mystacial vibrissae or by anaesthesia of the vibrissal pad, provided evidence, that facial tactile cues might be involved in the triggering and development of agg-

ression in mice. However, these studies were coarse, done in a too much restricted sense (e.g. only being interested in whether a reaction occurred or not, without differentiating in its quality) or using methods that clearly interfered with the animals' well being (such as enucleation or bulbectomy) and thus producing effects not only depending on simple sensory deprivation.

There seems to be only one profound example bringing behavioural, sensory physiological and neural data into close relation to describe a certain aspect of mouse behaviour in a neuroethological approach, i.e. pup-retrieving behaviour as studied by EHRET and his group. Using this model, he could characterize the motivational and perception mechanism to elicit maternal retrieving in behavioural experiments and revealed the necessary sign-stimulus. By presenting synthetic acoustic signals light could be shed onto the physiology of perception (i. e. a frequency-group filter mechanism in perception of sound signals could be shown) and the mutual evaluation as applied to the signal by the mouse (e.g. EHRET, 1983).

The present study is a step towards the same end using the somewhat different model of mouse aggressive behaviour. In particular the work to be described, attempted to answer the following Questions by adopting specific neuroethological Strategies as noted below.

1. Q: What are the behavioural units, relevant for the study of aggressive behaviour in mice and what problems are the sensory systems confronted with?

S: Observing mice under semi-natural as well as under cage conditions and describe aggressive responses in ethological terms.

2. Q: How are the senses of the mouse adapted to extract the relevant social environmental stimuli and what is their relative importance needed for the expression of aggressive behaviour?

S: Manipulating sensory input (sensory deprivation) of various modalities, singly or in combination and recording subsequent (altered) behaviour.

3. Q: What are the neural correlates for the formation of a certain behavioural motor output associated with aggressive beha-

viour?

S: Manipulating brain structures (brain lesions) and relating altered behaviour to lesions inflicted.

II. ANIMALS AND METHODS

1. Animals

All experiments were performed with male house mice (*M. musculus musculus*) of the LAC (Laboratory Animal Carshalton) strain, which was chosen because of its known territoriality (MACKINTOSH, 1973). Mice were obtained from the suppliers (Bromfield, England) at an age of 7-8 weeks and were maintained in groups of 20 individuals in makrolon cages (59x38.5x20 cm, type 4) until use.

To ensure, that the behaviour analysed is representative for mice in general, some experiments were repeated on F1-progeny of wild mice (*Mus musculus musculus*), caught at Toffen (Canton Berne) or on albino mice of the laboratory strain OF-1 reared at SANDOZ Ltd., Basle.

2. Behavioural analysis

To study mouse aggressive behaviour, two situations were chosen: 1. Territorial defense in enclosures and 2. Aggressive behaviour in cages.

2.1. Setup for enclosure experiments

These experiments were designed to study the structure of aggressive behaviour under semi-natural conditions (i.e. territorial defense in enclosures) and the role that various sensory cues play in it. Formation of territories essentially followed the method described by MACKINTOSH (1970). Mice were maintained under a reversed lighting schedule, i.e. white light from 20:00-08:00 hr and dim red light (5-7 Lux) during the intermediate period, room temperature was $20 \pm 1^{\circ}\text{C}$, humidity $60 \pm 2\%$. At 12 weeks of age, mice were marked with hair dye and allowed to form territories. This involved placing sets of 4 mice on both sides of a removable partition dividing a 2x2x1 m sheet-aluminium enclosure into two equal halves. Each enclosure was equipped with sawdust, food pellets, water bottles and small wooden or opaque plastic boxes affording the mice cover (Fig. 1).

In each enclosure a despotic dominance hierarchy developed on either side of the partitions, and when the latter were raised two months later, it was found

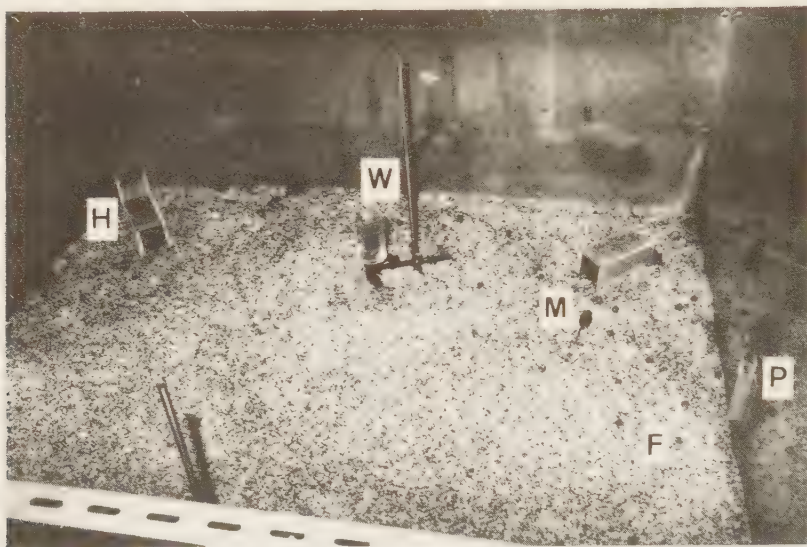


Fig. 1 Photograph of an experimental enclosure (in this case inhabited by wild house mice, *M. musculus*) providing a living space of $2 \times 2 \text{ m}^2$.

F: food pellet

H: house

M: mouse

P: slot to slide in partition

W: water bottle

that the dominant mouse from each half of the enclosure defended an individual territory. These territories were used for the experiments according to the procedure shown in table 1).

Each experiment consisted of 3 initial training sessions of 20 minutes carried out once a day on 3 successive days, and followed by 2 test sessions on the next 2 days. On training sessions, 5 group housed males (i.e. kept

together in a makrolon cage type 4 and used for at least 6 experiments of any deprivation type) were introduced simultaneously into an enclosure for 20 minutes. Territory holders usually chased and attacked the intruders which never fought back. Subordinate residents which tried to assist in territorial defense were themselves attacked by territory-holding mice and quickly withdrew to places of

procedure	deprivation type	recording
training session (3x)	----	protocol
test session 1.	no deprivation	video
test session 2.	deprivation/lesion	video

Table 1 Experimental design for enclosure experiments (for further explanations see text).

refuge. By the third such training session, the responses of dominant animals towards the intruders, and the responses of the intruders stabilized, i.e. the elements of aggressive behaviour as measured on successive days remained statistically unchanged. Test sessions were performed between 09:00 and 12:00, i.e. during red light, the procedure being the same as described for training, except that the agonistic behaviour of the territory holders was now recorded on video tape, using a camera (RCA, C2000, tube: ULTRICON 4833U, sensitive to light of approximately 0.2 Lux) mounted 1.2 m above the enclosures in an oblique position. In the first test session, the territory holders were undeprived of any sensory modality (control run). Twenty minutes before the second test

session the same animals were either acoustically deprived, visually deprived or both¹. Thus each animal served as its own control.

Since the procedure necessitated the repeated use of the enclosures, the contents of each were removed between use, and walls and floors washed with detergent to remove olfactory cues of previous enclosure inhabitants.

¹) For lesion experiments a slightly different method was used: Animals were singly introduced into the enclosure-halves following surgery. After 5 days of isolation, the training-testing paradigm was started, as described above (without removing the partition and only introducing one group-housed intruder at the time).

2.1.1. Evaluation of territorial behaviour

Behaviour of the territory holders under control and under each deprivation-condition was measured in terms of the following behavioural parameters (table 2), which provide an unambiguous description of the most relevant and conspicuous motor patterns as seen during territorial defense.

Each video-filmed 20 min. enclosure introduction was split into four 5 min. observation periods, during which the elements as described in table 2 were recorded using an improved

version of an apparatus previously described by HAUSAMANN and DIXON (1982). In short, each element was designated a key on a panel, pressing one of which during observation of video taped encounters, stored the duration (D) and frequency (F) of the observed behaviour on a data cassette which was later evaluated using a computer program.

For the evaluation of tracking trajectories, these were drawn on a transparent sheet (mounted on the TV-screen) using frame to frame analysis (video recorder Panasonic, NV

attend (att):	obvious (re)alignment of head to position of stimulus
approach (app):	moving (running) toward another mouse
chase (cha):	chasing of another mouse
successful attack (sak):	aimed attack and delivery of a bite
unsuccessful attack (uak):	misdirected attack without bite of conspecific
cross boundary (bnd):	crossing of territorial boundary
locomotion (lok):	all forms of mobility except cha, app, sak, uak, bnd
lose at boundary (lab):	termination of pursuit at territorial boundary
lose (lse):	termination of pursuit within territory after losing track of an intruder
stay (sta):	resting, or activities on the spot (i.e. eat, drink, etc.)

Table 2 Mouse ethogram as used for the evaluation of territorial aggressive behaviour displayed by dominant mice in enclosures.

730). This transparent sheet was then placed on an overhead-projector which was adjusted in projection-position such as to throw on the wall an image corrected for perspective distortion. This image was now redrawn onto paper and subsequently served as a template to measure off distances and angles (for details see Fig. 2).

Proximities between mice were measured off from the monitor screen. However, because of the oblique angle of the camera, such pictures were subject to perspective distortion. This was overcome by using a transparent grid of known scale and having the same distortion as the picture. By placing the grid over the screen, distances between mice were measured directly and, by referring to the scale of the grid then transposed into actual values.

2.2. Setup for cage experiments

Cage experiments were chosen to observe in detail close encounter aspects of aggressive behaviour as induced by isolation, i.e. cage aggressive behaviour (CAB)². The method as described in the following, is

well established and widely used, e.g. in ethopharmacological research (e.g. DIXON and MACKINTOSH, 1971; LAGERSPETZ, 1967; KRSLAK, 1976). A total of 44 mice, all at the same age of 12-24 weeks, were used in each experiment. 20 mice (designated as "intruders") were kept in a group cage (59x38.5x20 cm). 24 mice (designated "test-mice") were each isolated in a smaller cage (37x22x14 cm) until training began. All mice were maintained under effective external (day-night) light cycle, at a temperature of $20 \pm 1^\circ\text{C}$, the room not being controlled for humidity.

After the test-mice had been isolated for 14 days, training began. This consisted of three initial cage introductions during which one group-housed male was introduced into each isolation cage, every other day, for the

2) The term cage aggressive behaviour (CAB) is used in a general manner throughout this study, being aware, that the effects induced by isolation may be of various types, i.e. the "isolation-syndrome" was described by VALZELLI (1973) to show: 1. somatic effects (hyperirritability, hypertension), 2. behavioural effects (increase in spontaneous locomotor activity, compulsive aggressiveness, deviated sexual behaviour), 3. brain neurochemical effects (enzymatic alterations in cortex and subcortical structures).



Fig. 2 a) Example of a tracking protocol (which served as template, to measure off distances and angles), as obtained from frame to frame video-picture analysis and subsequent correction for distortion (grid-scale = 20 cm).

- — tracking animal (territorial mouse)
- — leading animal (fleeing intruder mouse)
(symbols every 40 ms)
- S = start, numbers refer to duration (s) of tracking

b) Measures taken to evaluate tracking behaviour

- θ_e error angle, the angle between the forward- (body-) direction of the tracking mouse and a line joining the two mice at a particular instant
- θ_f change-in-course angle, angle between two consecutive body directions of the tracking mouse, used to calculate ω_f , i.e. the angular velocity of the tracking mouse, by dividing θ_f by the sampling time (Δt , i.e. 40 ms).
- S_e distance between leader and tracker
- S_f distance between two consecutive positions of the tracking animal as used to calculate v_f , i.e. the forward velocity of the tracking animal while dividing S_f by Δt .

duration of 10 minutes. The 16 animals responding most aggressively towards intruders (as determined following the procedure described in table 3) were randomly assigned to one of two groups. The first group (8 animals) served as control (i.e. no sensory deprivation was carried out, however these mice were handled, anaesthetized etc., like group two animals). The animals of the second group were subjected to single or combined sensory deprivation (cf. section II.3). Deprivation was carried out between 12:00 and 16:00. The test was performed on the same day (except for olfactory deprived animals which were tested the day after deprivation) in red light

of 4 Lux at a time of day when external illumination had fallen beneath 1 Lux, i.e. in the evening. The test consisted of a 6 min. cage introduction (of an intruder-mouse, previously used for training, into each isolation cage) during which agonistic interactions of the two mice were recorded on video tape.

2.2.1. Evaluation of aggressive behaviour in cages

Since there was some variability in aggression (probably due to variable motivation-status, previous social rank, etc.), displayed by the test mice, they were subjectively classified during the last training, using the following scorings:

behaviour of test mouse	score
- a high degree of aggression (more than 10 bites delivered to the intruder during 10 min.)	3
- an intermediate degree of aggression (2-10 bites delivered in 10 min.)	2
- a low degree of aggression (0-1 bite in 10 min.) and "aggressive grooming" of intruder	1
- no aggressive behaviour (no signs of aggression according to the above criteria)	0

Table 3 Scoring used to classify isolated mice (in terms of aggressiveness) and to select them for the study of cage aggressive behaviour (CAB).

category (abb.)	elements (abb.)
non-social behaviour (NSO)	explore (ex), scan (sc), leave (lv), wash (wa), self-groom (sg), scratch (sr), dig (dg), push-dig (pd), kick-dig (kd), shake (sh), jump (jp), eat (ea), drink (dk), sit (si), substrate (su), stretched attend posture (sp)
social attention (SAT)	attend (at), stretched attend (sa), approach (ap), turn (tu)
social contact (SCO)	investigate (in), nose (no), groom (gr), sniff (sn)
sex-related behaviour (SEX)	follow (fo), attempted mount (am), mount (mt), genital-groom (gg), push under (pu), crawl over (co), push past (pp)
aggression (AGG)	threat (th), attack (ak), bite (bt), chase (ch), aggressive groom (ag)
offensive ambivalence (OFA)	offensive sideways posture (os), offensive upright posture (ou)
defensive ambivalence (DEA)	oblique (ob), upright posture (up), defensive upright posture (du), defensive sideways posture (ds)
distance ambivalence (DIA)	zig-zag (zz), circle (ci), walk-round (wr), rattle (ra)
arrested flight (ARF)	crouch (cr), freeze (fr), kick (kk)
escape (ESC)	flag (fg), evade (ev), retreat (rt), flee (fl), on bars (on)

Table 4 Ethogram as used for the evaluation of aggressive behaviour in cages. Elements are self explanatory by their definition, for further comments see text.

Usually about one forth of the isolated mice displayed a low degree of aggression towards intruder mice or no aggressive behaviour at all. These were not further used in the experiment.

For the detailed analysis of CAB an adapted version of the ethogram introduced by GRANT and MACKINTOSH (1963) and modified by DIXON (1986) was used. This ethogram (table 4) consists of distinct behavioural elements, i.e. postures (static) and acts (involving movement), classified into categories due to their motivational similarities, and considering their relationship in occurrence during particular response patterns.

The behaviour of the resident mouse was commented on a tape recorder in terms of the elements contained in table 4. From the tape recorder the elements were then transferred to the computer by pressing the corresponding key on an adapted keyboard of the same apparatus as described in section 2.1.

3. Deprivation techniques

In general two ways are conceivable to characterise the sensorial events underlying the observed behaviour: a) enriching

the mouse environment with cues of the modality to be studied, b) depriving the animal in test of the sensory modality to be examined with respect to its importance. In the present work the second approach was chosen exclusively. Great care was taken to cause the least possible discomfort to the animals, and emphasis was placed on reversibility of the deprivations carried out. The techniques used were either adapted from the literature or especially conceived for this study and their efficacy and advantages or drawbacks will be discussed in section IV.5.

3.1. Olfactory deprivation

For olfactory deprivation a modified version of the method first described by ALBERTS and GALEF (1971) was used. Mice were anaesthetized with NEM-BUTAL (50 mg/kg, i.p.) and placed on their back upside down on a section-tray. A silicone tube was then introduced into the mouth (which was held open by a pair of tweezers) and a vacuum applied to it. Now ZnSO_4 (5%, dissolved in saline) was applied drop by drop at the external nares and sucked off through the mouth until two drops had been

flushed through each nare. Mouth and nares of the treated mouse were aspirated 3 times, in 15 min. intervals. Then the mouse was put back into its cage. (In control animals, the mucosa was flushed with 0.9% saline, the procedure otherwise being the same as stated above). This method was the most delicate one both in terms of reliability and reversibility, however results will show, that such treated mice did not seem to suffer from intoxication, as has sometimes been argued against this method (SIECK and BAUMBACH, 1974).

3.2. Acoustic deprivation

Acoustic deprivation was effected by earplugs (i.e. KNUDSEN and KONISHI, 1979). Silicone rubber (SILASTIC 734 RTV, Dow Corning, USA) was injected into the ear of the anaesthetised (Halothane) mouse and after drying blocked the external auditory meatus (control animals received only anaesthesia). The effect of earplugs was tested behaviourally by recording startle- and pinna-reflex (e.g. SHNERSON and PUJOL, 1983, p. 416) in response to an acoustic stimulus, i.e. clapping hands. Both reflexes were absent

in the deprived state. After test sessions the earplugs were easily removed with a pair of tweezers.

3.3. Visual deprivation

Visual deprivation was performed by fitting the mice with opaque scleral contact lenses as conceived and designed especially for this study.

First a template was prepared (Fig. 3a). For this, one LAC-albino mouse (matching the test animals in weight) was sacrificed and enucleated. The eyes were then rinsed in 0.9% NaCl solution and cast in epoxy two component resin (RUCO, Rupp and CO. AG, SWITZERLAND), the cornea facing downward. The resin was left to dry and harden during the night. The epoxy block was then filed down to the rear rim of the cornea so that the eye could easily be removed. To apply a vacuum, a 0.4mm hole was drilled through the middle of the resin until it reached the eye mould. To form contact lenses, a square of cellulose acetate foil (ULTARAPHAN 0.07 mm, Lonza, Germany) was placed over the open end of the template and heat-moulded. The lenses were trimmed with a specially designed knife and covered on the

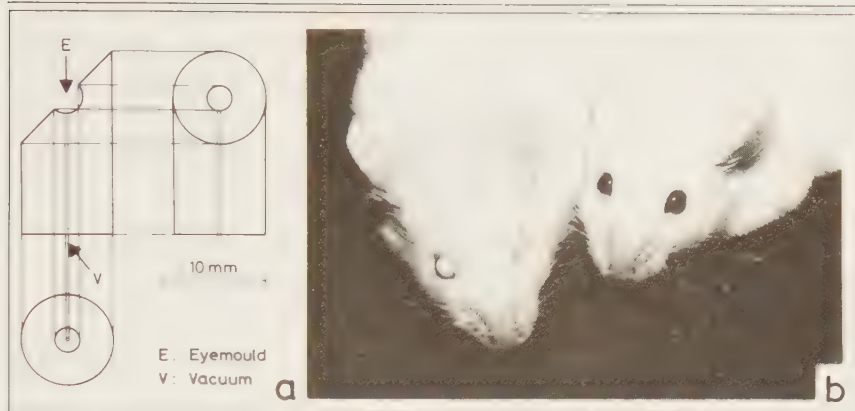


Fig. 3 a) Sections of the template used to form contact lenses.
b) Mouse wearing opaque contact lenses (left animal) and control animal (right).

inside with a layer of TIPP-EX fluid (Tipp Ex Vertrieb GmbH and Co. KG, Germany). Opacity was tested in a spectroscope LAMBDA 3 (Perkin Elmer, USA) and the extinction proved to be more than 5 log-units throughout a range from 350 to 750 nm, i.e. the lenses were virtually opaque. Lenses were fitted in mice lightly anaesthetised with Halothane (control animals received anaesthesia without further manipulation).

3.4. Vibrissal deprivation

To effect vibrissal deprivation, test-mice were slightly anaesthetized with Halothane. In animals to be deprived, the vib-

rissae on the muzzle were carefully cut bilaterally with a pair of scissors (in control animals a small patch of fur caudally to the vibrissal arrangement was superficially shaved off).

4. Lesion technique

Lesions were performed under pentobarbital anaesthesia (Nembutal, 50 mg/kg, ip) in a stereotaxic apparatus using electrocoagulation techniques (current: 1.8 mA, voltage: 35 mV, time: 30 s). The lesions were placed according to the coordinates given in the stereotaxic atlas by SLOTNIK and LEONARD (1975). Fig. 4 shows 3-dimensional reconstruction of part

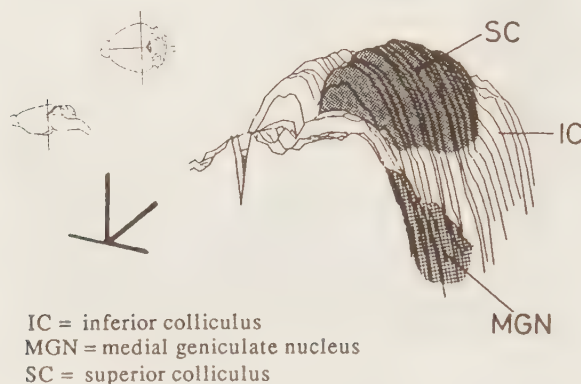


Fig. 4 Three-dimensional reconstruction of brain structures (post. thalamus and midbrain) where test-lesions were placed (shaded areas), cortex removed. Scale: 0.5 mm, most frontal section is 2.00mm post. bregma, sections every 0.1mm, cf. Fig. 5. **Inset:** top- and side-view of mouse brain: lines indicate the place of most frontal section, the SC is marked in black.

of the midbrain tectum and the posterior thalamus. The brain structures to be lesioned in this study are shaded.

5. Histology

5.1. Analysis of brain lesions

After the lesion-experiments, these mice were sacrificed for histological investigation. Therefore, mice were perfused with 4% formalin by the heart. Brains were then fixed in the same solution for 4 days, then they were cut, using a freeze-microtome (FRIGOMAT, JUNG GmbH, Germany). The obtained 18μ thick slices were mounted on a slide, which was covered with egg-albumin, and preserved in 70% alcohol until staining with

cresyl-violet and sealing according to the following procedure³ (for solutions see⁴):

3) 1. discard alcohol 70%, 2. water (5min.), 3. rinse in distilled water (twice), 4. stain (ca. 20min.), 5. rinse with 95% alcohol (twice), 6. dehydrate in ethanol abs. I (10min.), 7. dehydrate in ethanol abs. II (10min.), 8. differentiate in carbol-xylol I (shake slices and watch carefully), 9. differentiate in carbolxylol II (until desired differentiation is reached), 10. clear in xylol (3x) (10min. each), 11. seal in eukitt.

4) staining-solution: first a stock-solution of 2g cresyl violet dissolved in 250ml distilled water, is prepared. Two days later 250ml of aethanol 96% are added to it. This stock-solution is then filtered and is diluted 1:1 with distilled water. Carbol-xylol(I,II): 100ml phenol is dissolved adding xylol ad 1lt. 4% formalin: 65% formalin is dissolved in 0.9% saline.

These prepared sections were then used to reconstruct the proper lesion sites by comparing them with the corresponding section-plates in the histological mouse brain atlas (SLOTNIK and LEONARD, 1975) and marking the lesions in the standardized mouse brain as displayed in Fig. 5.

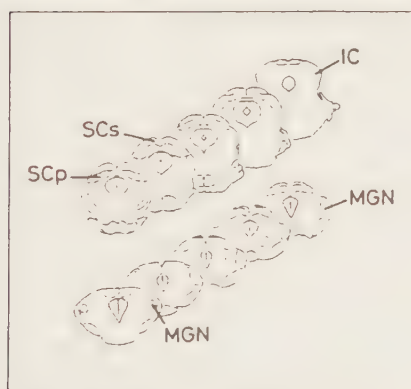


Fig. 5 Standardized mouse brain, used to reconstruct lesions. (sections are taken 2.7, 2.9, 3.1, 3.4, 3.5 // 3.7, 4.0, 4.2, 4.6 and 4.9 mm post bregma).

IC=inferior colliculus, SCs=superficial layer of superior colliculus, SCp=deep layer of superior colliculus, MGN=medial geniculate nucleus.

5.2. Analysis of olfactory mucosa

Nasal cavities of mice treated with ZnSO_4 were decalcified (SMITH, 1982) electrolytically, sectioned at 5 microns and stained with Haematoxylin-Eosin.

Additionally, Bodian silver and PAS stains were also applied to selected sections. At least 2 sections from each nasal cavity were examined.

6. Sonographic recordings

Recording of the rustling-noise caused by mice running in saw dust (i.e. the acoustic bases for acoustic tracking) was done using a condenser microphone (Bruel & Kjaer, cartridge type 4135, (held at a distance of ca. 15cm above the walking or fighting mice)), and a tape recorder (PHILIPS, -analog 714) operated at a recording speed of 15 inch/s. Visualization of the sonograms was achieved, using a sonograph (B/65, KAY ELECTRICS CO., Pine Brook, N.J.).

7. Preparational and statistical data analysis

7.1. Smoothing crude data

For the mathematical evaluation of the territory holder's tracking-trajectory in relation to the intruder's flight path, crude data as obtained from the frame to frame video film analysis (cf. II.2.1) were smoothed. This was done, using a 5-point non-distorting running-average smoothing formula (HILDEBRAND,

1977). This procedure acts like a low pass filter on the behavioural data, cancelling out the high frequency part of the data set (i.e. noise).

7.2. Wilcoxon-test (test-measure = T)

In enclosure experiments, test animals served as their own controls. Consequently, to compare the mean frequencies and durations of elements under various conditions of deprivation vs. controls, the non-parametric Wilcoxon matched-pairs signed-ranks test for dependent samples was used (SIEGEL, 1956). The null-hypothesis was rejected at a two tailed significance level, with $p < 0.05$.

7.3. Mann-Whitney U test (test-measure = U)

This nonparametric test for independent samples (SIEGEL, 1956) was applied to compare the mean frequencies and durations of elements as evaluated in the cage-introduction experiments, the null-hypothesis being rejected at a two tailed significance level, for $p < 0.05$.

7.4. t-Test (test-measure = t)

The parametric t-Test served the comparison of mean-values of two independent samples (SA-CHS, 1983). This formula was for example used to compare mean proximities between mice when detection or attack took place under semi-natural conditions, i.e. in enclosures. Again the level of significance was set two tailed, for $p < 0.05$.

7.5. χ^2 -Test (test-measure = χ^2)

This test was used, to calculate whether observed distributions deviated significantly from an expected one, e.g. for transition probabilities between behavioural elements in enclosure experiments. Level of significance, two-tailed, for $p < 0.05$.

III. RESULTS

This section is divided into the two principal parts A and B: The first part focuses on agonistic behaviour under seminatural conditions, i.e. Territorial Aggressive Behaviour (TAB) in enclosures, (cf. II.2.1.) while the second part deals with aggressive behaviour as seen during close encounters, (cf. II.2.2), i.e. Cage Aggressive Behaviour (CAB).

PART A: ANALYSIS OF AGONISTIC BEHAVIOUR IN TERRITORIES

In section 1 of this chapter the behavioural aspects of territorial defense are analysed, and in section 2 the relative role of vision and audition in this type of behaviour is investigated. On the bases of these findings a sensory-physiological characterization of some phases of the territorial response is attempted in section 3. Finally, in section 4 a neural correlate of tracking behaviour will be developed.

1. The behavioural structure of territorial defense

Since the complete mouse-ethogram as used in cage experiments did not seem to meet the special demands of enclosure experiments (e.g. no territory-border effects occur in cages), the study was started with extensive observations of territorial behaviour as displayed by territory holders (=dominants) upon introduction of intruders, i.e. the classical approach of descriptive ethology was applied, which yielded a list of the most conspicuous and most relevant motor patterns (= behavioural elements) as presented in table 2. An analysis of the occurrence of these elements in terms of their absolute frequency and duration, per 5 min. observation period is presented in Fig. 7. Locomotor activity- (lok) and rest elements (stay) were the most frequent elements and accounted for 5/6 of the observation time, the elements (sak, uak, cha, los, bnd, lab) forming the remainder. Trackings (=chases) occurred at a mean frequency of 13 events per 5 min., with a mean duration of about 2s each (the longest tracking observed, lasted for 6s). Fig. 7 will subsequently serve as reference for the deprivation ex-

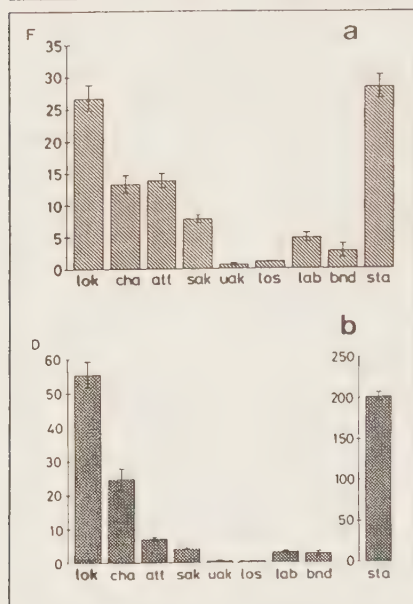


Fig. 7 Occurrence (mean $\pm$ SEM) of the elements defined to describe territorial aggressive behaviour, in terms of absolute frequency (F, Fig. 7a) and absolute duration [s] (D, Fig. 7b) as recorded during the standard observation period of 5 min. ($N_{\text{animals}}=27$, $N_{\text{observation periods}}=108$). For the definition of the elements see table 2).

periments, where the occurrence of the most important of the above elements will be expressed in % of the corresponding maximal values.

The dynamic relationships between the relevant behavioural elements, as determined by sequence analysis, is given in Fig. 8 and this yielded the following

major pathways characterizing territorial defense behaviour:

Shortly after introducing the group-housed male mice (intruders) into the enclosure, the territory holder displayed behaviour characteristic of territorial defense. It began running to and fro, sniffing at the substrate as though in search of something [i.e. this phase will subsequently be termed: arousal- or motivation-phase]. Thus stimulated dominants typically attended to any acoustic or visual cue provided by a conspecific in their surroundings (indicating their detection) and localized it (seen as alignment of head or/and body to the intruder) [i.e. termed detection/localization-phase]. Then territory holders approached the intruders [i.e. termed approaching-phase] and, upon the latter's withdrawal tracked (= chased) them [i.e. termed tracking-phase] until either they left the territory or, if not, until the intruders were attacked by the territory holding male [i.e. termed attacking-phase], which could be distinguished from the preceding tracking-phase by a sudden speeding up of the tracking mouse, leading to the final clash with the intruder.

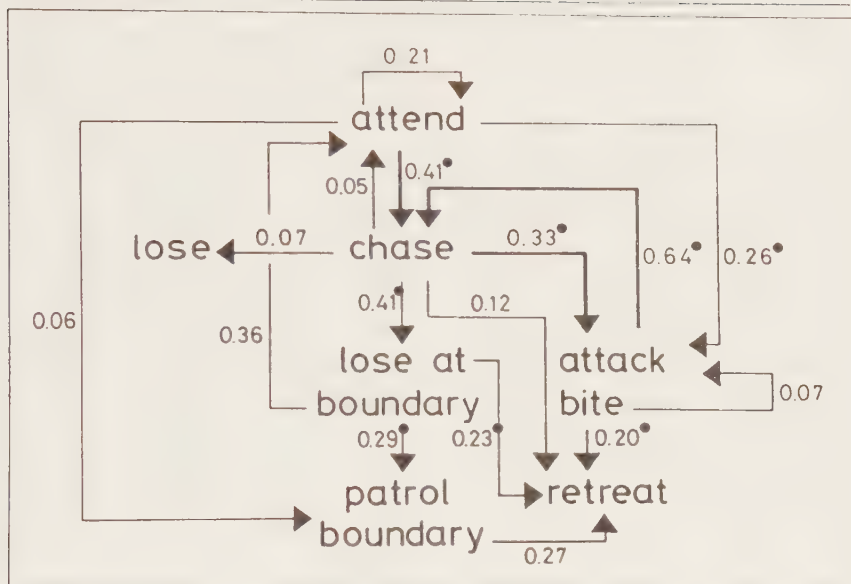


Fig. 8 Sequential relationship between the behavioural elements as occurring during a typical response of a territory-defending mouse towards an intruder animal. The transition values (i.e. probabilities for succession from one element to another) are given in % (1 = 100%). The emphasized arrows represent the most typical social interaction path.

• transition-probabilities higher than expected by chance ($p < 0.05$).

Intruder mice were never observed to fight back, but showed exclusively elements of submissive-behaviour or active flight (cf. categories DEA, ARF and ESC in table 4). The same held true for subordinates living in the enclosures.

2. Effects of sensory deprivation on territorial defense behaviour

An animal's peripheral sensory equipment is very obviously shaped by its ecological niche (COLLETT, 1983) and there is no reason to assume, that this is not the case in the nocturnal mouse. Thus having established the fundamental ethological aspects of mouse territorial aggression, deprivation experiments were con-

ducted to evaluate the sensory correlates of this behaviour.

2.1. Acoustic deprivation

In these experiments 9 territory holders were provided with silicone-rubber earplugs which had several effects on the behaviour of these mice (Fig. 9):

Regarding the relative frequency of successful and unsuccessful attacks, no difference between controls and acoustically deprived animals could be found. The same holds true for the time

spent by a mouse in its own territory ($T > 12$, $p > 0.05$). Acoustically deprived territorial mice, however showed a remarkable increase in locomotion, reaching statistical significance ($T = 3$, $p < 0.02$). This finding will be discussed in view of a possible motivational mechanism for aggressive behaviour in section IV.2. Furthermore, "attends" were strongly reduced ($T = 0$, $p < 0.01$), indicating a prime importance of audition in detecting intruder animals. The most striking fin-

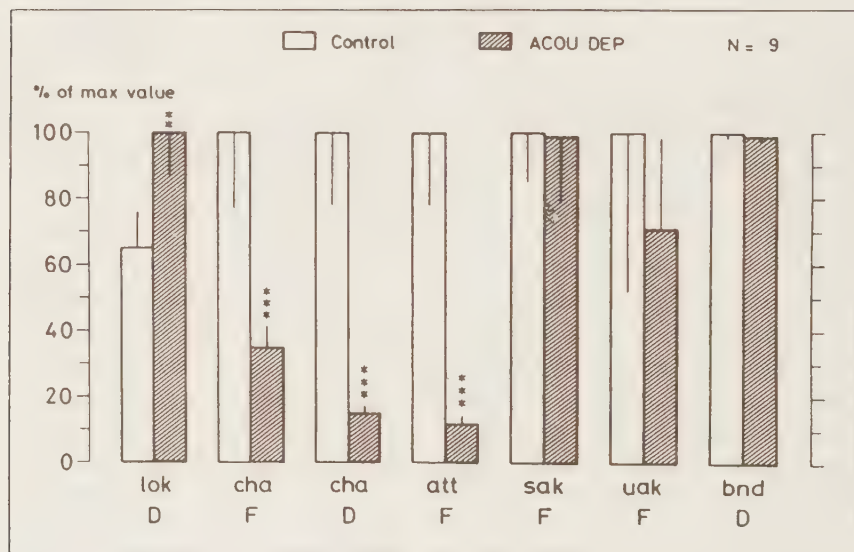


Fig. 9 Effects of acoustic deprivation on the aggressive response of territorial male mice. Mean frequency and duration ($\pm$ SEM) are expressed as %-values of corresponding maximal test- or control values; * $p < 0.05$, ** $p < 0.02$, *** $p < 0.01$.

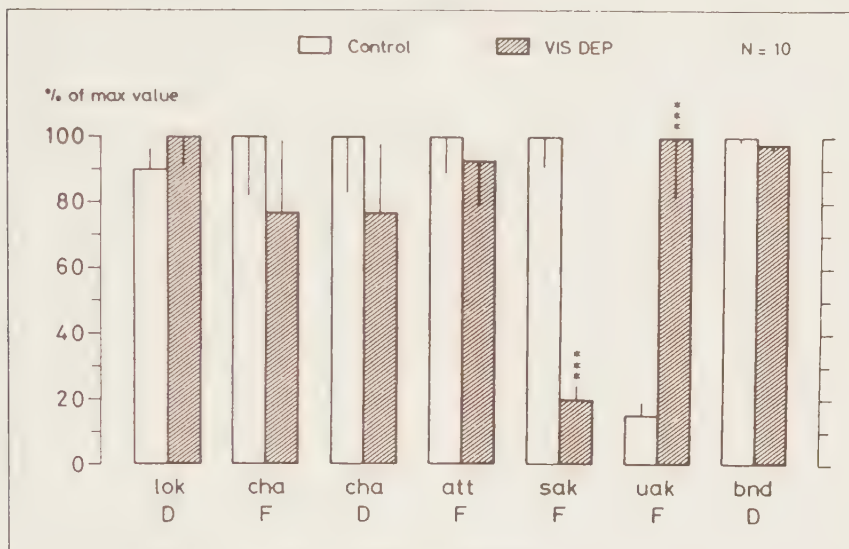


Fig. 10 Effects of visual deprivation on the aggressive response of territorial male mice. (For further explanations see legend of Fig. 9).

ding in this series of experiments was however the marked reduction in the frequency and duration of chases. Furthermore, the chases ended with a "lose" in $83 \pm 8\%$ (mean $\pm$ SEM) of the observed cases (control value $8 \pm 2\%$).

2.2. Visual deprivation

The results shown in Fig. 10 depict the effects of visual deprivation, as effected by means of contact lenses, on agonistic behaviour. No significant changes were found in locomotion, attends and crossing of the territorial

boundary ($T > 10$, $p > 0.05$). Furthermore, duration and number of chases were not significantly affected by visual deprivation ($T > 10$, $p > 0.05$). This remarkable result corresponds to the above finding, that acoustic deprivation had a major effect on chasing, and demonstrates, that mice must possess a neural mechanism linking acoustic input with motor output suitable to chase a conspecific. Successful attacks were significantly diminished in visually deprived animals ($T = 0$, $p < 0.01$), whereas unsuccessful

attacks reached a higher level ($T=0$, $p<0.01$).

2.3. Combined acoustic and visual deprivation

Although from a comparison between the results shown in Fig. 8 and those obtained with deprived animals (Fig. 9 and Fig. 10) it can be seen, that acoustic and visual deprivation affect territorial behaviour to quite differing degrees (i.e. vision and audition obviously play different roles during the territorial response sequence), some attacking in visually deprived animals

(Fig.10) and, to a lesser degree, chasing behaviour in acoustically deprived animals (Fig. 9) was still present. Thus the results obtained may have been influenced by contributions of senses other than vision or audition, e.g. olfaction or sense of touch. Since a pilot study had shown that no graded effects on territorial defense can be obtained by olfactory deprivation directly (such deprived animals showed no aggressive behaviour at all (see also part B, Fig. 29) and were found to lose their dominant status within 24 hours) a different

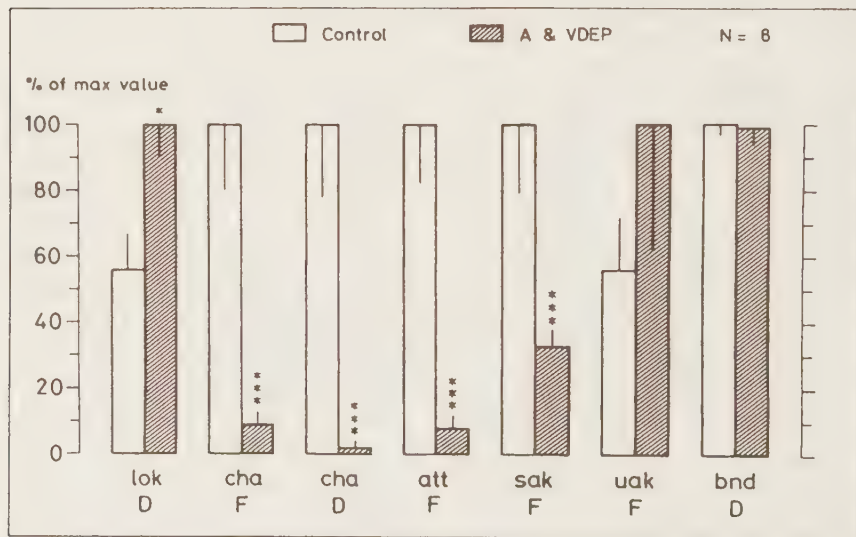


Fig. 11 Effects of combined acoustic and visual deprivation on the aggressive response of territorial male mice. For further explanations see legend of Fig. 9).

course was followed, i.e. it was assumed that in territory holders deprived of both vision and audition would reveal the relative contributions of the remaining senses.

Eight animals were tested in this combined deprivation state and Fig. 11 shows the results. As can be seen, no changes were found in the time a territory holder spent within its own boundaries ($T=9$, $p>0.05$). Attending- and chasing behaviour were almost completely absent and were observed to occur only when an intruder was within touching distance of the territorial animal. (It might be argued here, that animals deprived of audition and vision may have lost their motivation for territorial defense. This is however not the case. Such deprived animals spent a lot of time patrolling their territory (expressed by the significantly increased locomotion ($T=2$, $p<0.05$)) and upon gaining contact with intruders, vigorously attacked them. Successful attacks were less frequent ($T=0$, $p<0.01$) in deprived animals as compared with controls. No difference was found regarding unsuccessful attacks ($T=9$, $p>0.05$). Thus, while it is now clear that for

tracking (chasing) no other modality than vision and audition must be considered a considerable amount of attacking behaviour persisted in animals receiving combined deprivation. Whether this is to "assign" to tactile or olfactory input will become clear after the next section, when the effective distances of the various sensory modalities will be considered.

3. Sensory-physiological characterization of some behavioural phases associated with territorial defense

The results so far show, that the aggressive response of territory holders can be divided into 5 distinct behavioural phases and that these are differentially affected by various sensory deprivation. In this section, some of these phases are analysed in detail, to investigate the capacities of the various senses and the underlying neural networks.

3.1. Attending behaviour - effective distance of the various sensory modalities

Attending (i.e. orientation of the head- and/or body towards the direction of a conspecific) was found to be the first sign indica-

ting that the territorial animal had detected an intruder. Thus, attending behaviour under various sensory deprivation conditions may be used to assess the effective distance over which a given modality operates (e.g. the mean maximal distance over which an acoustic cue can elicit an attend-response).

To validate this assumption the effective distances of audition, vision and olfaction were calculated, using the critical proximities between mice when the element "attend" was displayed by the territory holder under various deprivation conditions (thus attending behaviour is

immediately related to relative⁵) sensitivity of the senses. The measures given in Table 5 were obtained with the grid procedure, (cf.II.2.1.1).

As can be seen, the most effective cues in eliciting the "attend-response" were acoustic stimuli, i.e. the mean maximum effective distance over which audition worked in this enclosure

⁵Relative means, that the response is not only reaction specific, (i.e. associated with territorial aggression) but also depending on the sensory cues provided by the intruders and their actions (e.g. visual contrast of an intruder against background or rustling noise made by intruders in saw-dust).

	distance for "attend"	
	moving intruder	stationary intruder
non-deprived dominant	71.4±22.9	8.9± 3.0 [!]
acoustically deprived dominant	18.0± 3.2 [*]	10.5±2.2 [!]
visually deprived dominant	70.1±17.3	--- [!] *
acoustically and visually deprived dominant	--- [*]	--- [*]

* significantly different from non deprived dominant (t-test, $p < 0.01$ two tailed).

[!] significantly different from moving intruder (t-test, $p < 0.01$, two tailed).

--- "attend" occurred only when the dominant was within touching distance of an intruder.

Table 5 Critical proximities (mean±SEM in cm) between territory holders and intruder animals for the former to show the element "attend".

situation was about 70 cm (the greatest distance measured was 110 cm). Visual sensitivity as obtained from acoustically deprived territory holders, showed that the response of the test-mouse depends on whether the intruder was moving or keeping still. In the former case the effective distance is with around 18 cm about twice the one found in the latter case, being about 10 cm. Animals with combined deprivation showed only very few "attends" and were observed to do so only when they were within touching distance (i.e. the tactile sense provided the necessary input) of an intruder. This is good evidence that senses other than vision or audition, i.e. olfaction, do not appear to be effective in exploiting distant cues.

Consequently, the relative frequency of the element "attend" as observed during the various deprivation conditions seems to mirror the relative importance of the 3 senses in eliciting this behavioural element (audition: 88%, vision 7%, tactile sense, 5%).

3.2. Tracking behaviour (=chasing)

Tracking behaviour, during which the territorial animal pur-

sues an intruder with remarkable accuracy for several seconds, was the most conspicuous phase occurring during territorial aggression, thus special attention was dedicated to its analysis.

3.2.1 Acoustic tracking

The experiments in chapter III.A.2.1. provided evidence that tracking is acoustically mediated. In order to unravel the underlying neural control system, trackings of bilaterally visually deprived territory holders were evaluated. (Fig. 12, shows examples of acoustic tracking behaviour).

Whenever a conspecific (intruder) came within 40-60 cm of the territorial mouse, it was chased (i.e. tracking ensued). Results of all animals were consistent (14 trackings from 6 animals, i.e. 48 sec. of pursuit were analysed) and a general description of acoustically mediated tracking is given on the basis of the example shown in Fig. 14 (corresponding values for the whole data set are given in brackets). The pursuer seems to keep a constant distance from the intruder, the mean value being 47 ± 12 cm (42 ± 11 cm for vis-dep animals, 29 ± 8 cm for controls, 19 ± 6 cm for acou-dep

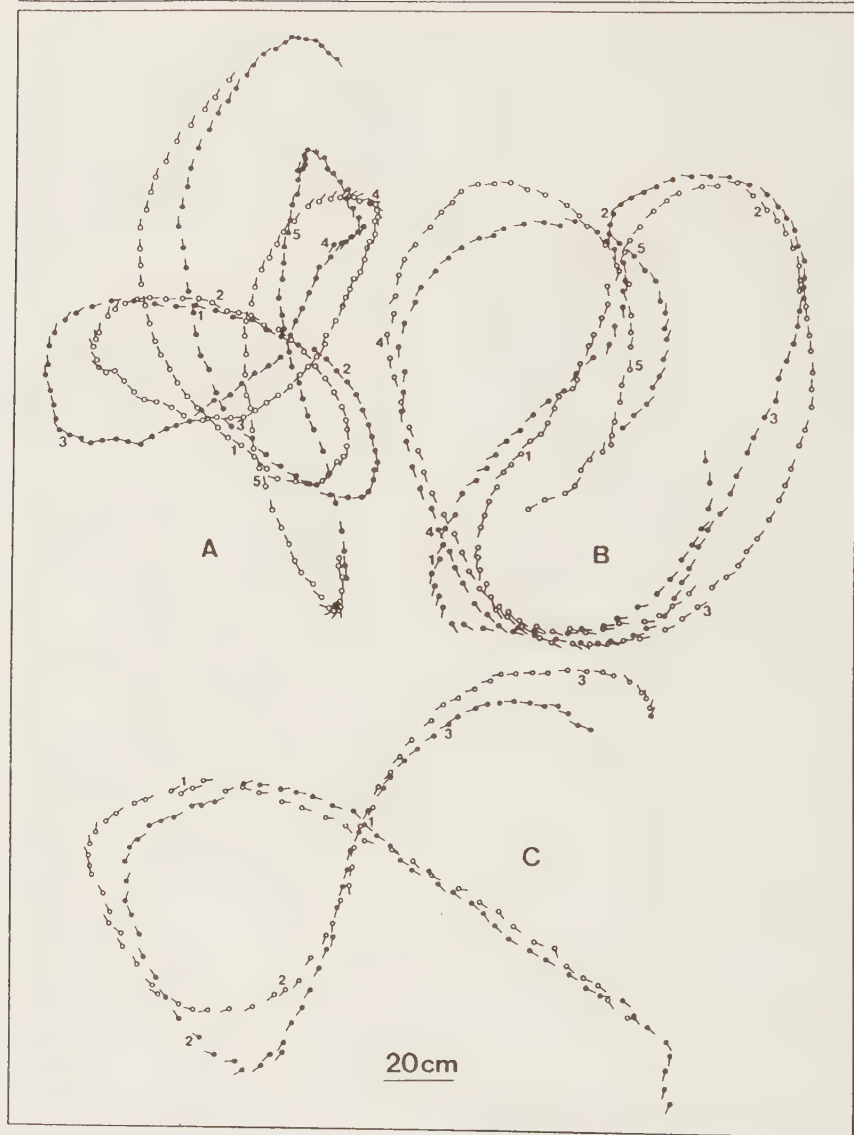


Fig. 12 Examples of acoustic tracking trajectories, for explanation of symbols see Fig. 2. (scale = 20cm)

animals). When the pursuer's body axis is in line with the intruder and at a distance of 30-40 cm, the territorial mouse accelerates (arrows in Fig. 14) to reduce the distance to the escaping mouse up to a point where vision would be expected to take over (18 ± 3 cm, cf. table 5) and finally guide the attack. During these acceleration phases the forward velocity of the tracking animal is about 1.4 times that of the leading mouse (intruder). The only way for the intruder to escape is therefore by making a turn, which, because of the trackers inability to follow each turn instantaneously, again increases the

distance between the two. Trackings are seen to cease either on the territorial boundary, when the intruder leaves the territory or when the intruder stops moving. The latter observation is indicative of two things: 1. acoustic tracking is a passive mechanism relying on the intruder's noises⁶ (therefore we define tracking behaviour here as passive acoustic tracking, (PAT)) and 2. it is functioning only under closed-loop conditions (i.e. continuous acoustic feedback from the stimulus is needed to maintain tracking). Inspection of Fig. 14 shows, that the course of the pursuer is closely asso-

⁶) There are two principally different sources as to the acoustic stimuli used by the territorial mouse for tracking: They could either be the echoes of sounds generated by the tracker itself (in analogy to the ultrasonic "peillaute" sent out by bats, e.g. GRIFFIN, 1958) or the noises made by conspecifics moving about on the saw dust (in analogy to the acoustic hunting system of the owl; PAYNE, 1971). The above finding suggests that the latter possibility is the one exploited by the mouse. Therefore in Fig. 13 the frequency-spectrum of intruder-caused rustling noises in saw-dust is given.

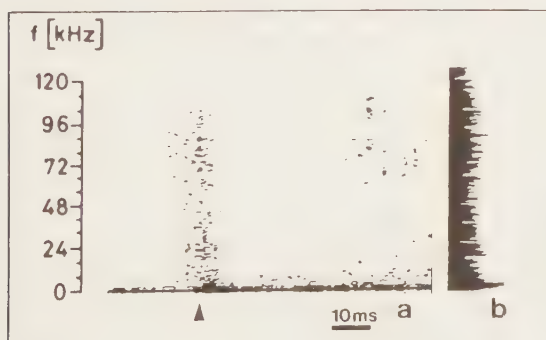


Fig. 13 Phonographic recording of rustling noise made by intruders moving in saw-dust (a), relative intensity distribution (over the whole frequency band) of the rustling incidence marked with an arrow in (a) (b).



Fig. 14 Representative example of an acoustic tracking trajectory that serves the general description of acoustic tracking. For explanation of symbols see Fig. 2, arrows indicate acceleration phases and subsequent overshoot of the leader's course by the tracking animal (scale = 20 cm).

ciated with that of the intruder, suggesting that the control system for PAT is continuous rather than consisting of standardized manoeuvres in answer to the evasive actions of the leader. One obvious possibility for the pursuer would be to evaluate the error angle θ_e between its own body axis and the relative direction of the fleeing intruder and transform this value into an

appropriate angular velocity ω_f , (i.e. the angle in course change during 40 ms sampling time) for a turn towards the leader's position. To test this hypothesis, θ_e and ω_f were plotted every 40 ms, measured as shown in Fig. 2. Fig. 15 reveals that, indeed, the pursuer answers a given θ_e with a matched ω_f after a certain time lag. ω_f is assigned to the first of two consecutive measures of the

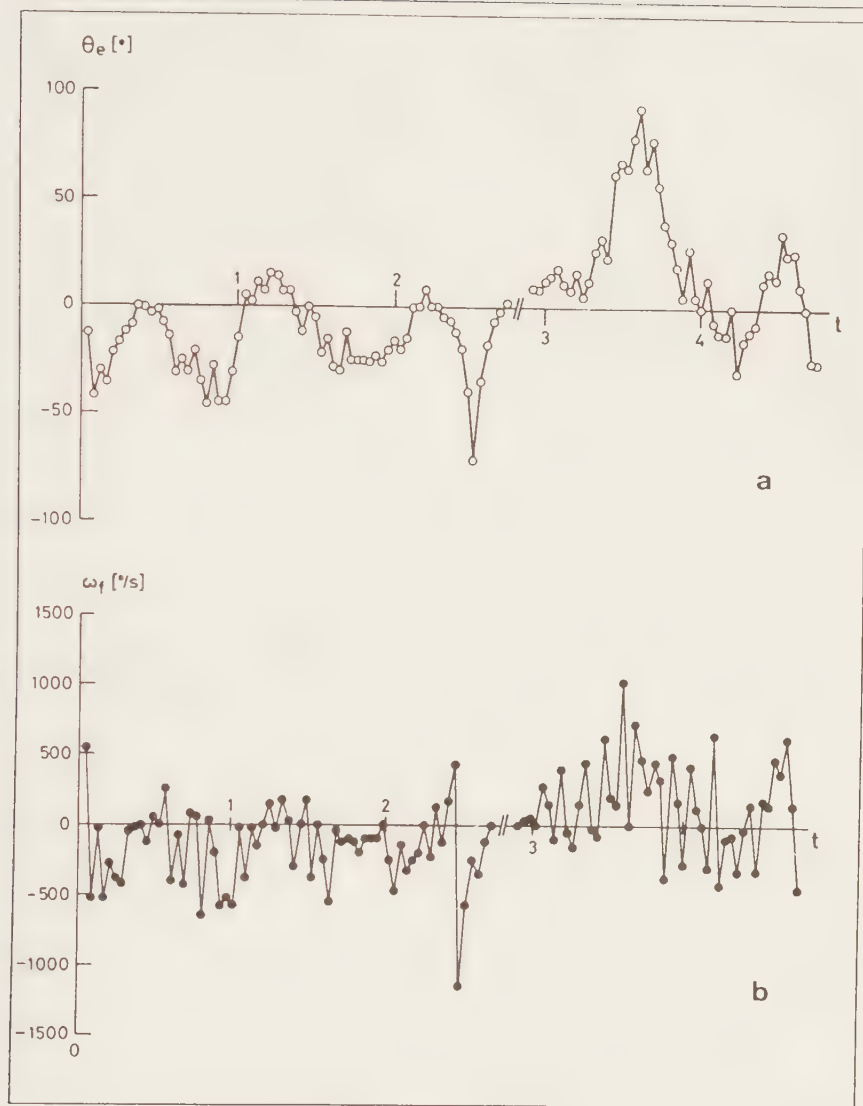


Fig. 15 Plots of error angle θ_e (a) and the angular velocity ω_f (b) during the tracking shown in Fig. 14. Numbers on the time axis refer to the numbered points in Fig. 14 (i.e. seconds of tracking).

direction of the body axis, (i.e. advanced by about 20 ms). However, the body axis (also the head, but this is hard to be recognized on the video pictures) seems to oscillate about the actual course which renders the calculation of certain measures, such as the time-lag and the factor used by the tracker to transform θ_e into ω_f , somewhat tedious.

To overcome this problem we applied the HILDEBRAND non-distorting curve-smoothing computer program to the set of data. This program works like a low-pass-filter on the data. Fig. 16 shows the result. It can be seen that the angular velocity curve mirrors the error angle curve (Fig. 16), the time lag between input (θ'_e) and output (ω'_f) - as can be seen from the inset of Fig.

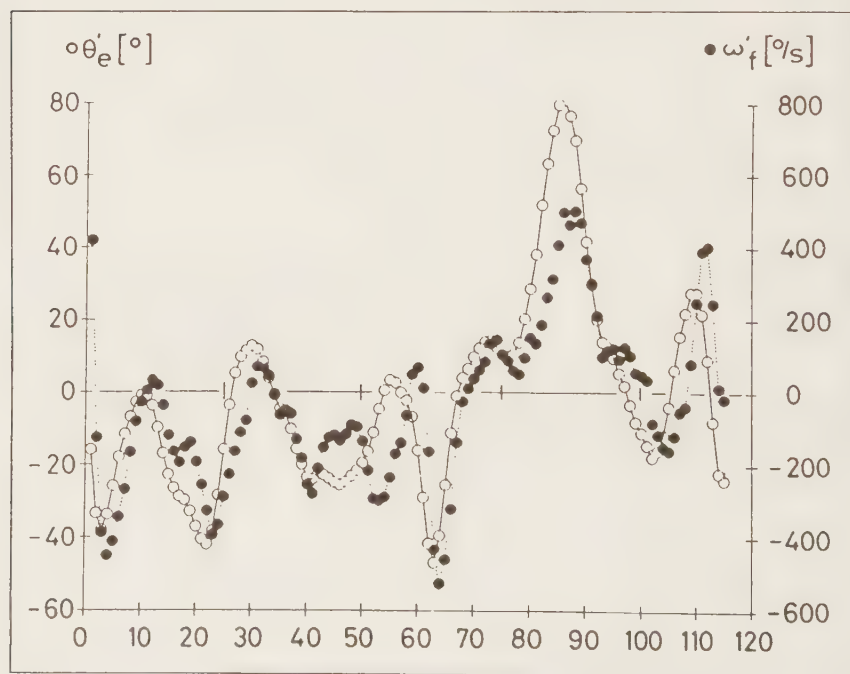


Fig. 16 Plot of error angle (○) and angular velocity (●) after application of the HILDEBRAND non-distorting curve smoothing program. Numbers on the abscissa refer to value numbers (i.e. taken every 40ms) and marks on the zero-line are inserted every second (i.e. refer to the numbers in Fig. 14). The angular velocity curve mirrors the error angle curve, showing a certain time lag.

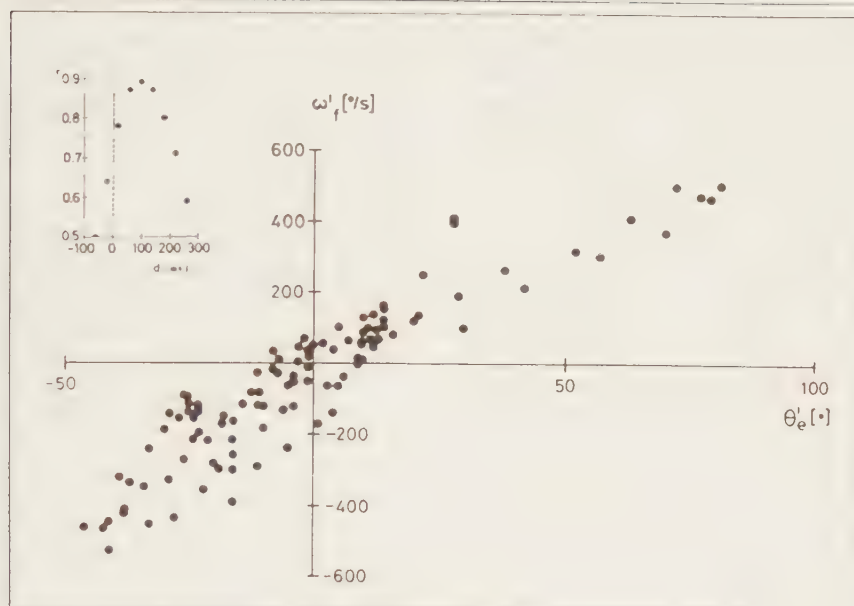


Fig. 17 Scatter diagram showing the relationship between θ'_e and ω'_f (smoothed values). The delay time has been taken as 100ms, as is suggested in the inset, which displays the correlation coefficient (r) in relation to various assumed delay times (d).

17 - being around 100 ms (considering that ω_f is assigned to the middle of the sampling time, i.e. advanced by about 20 ms). Inspection of Fig. 17 reveals an apparently linear relationship between θ'_e and ω'_f . The scatter diagram is based on the assumption that the input variable θ'_e maximally affects the output variable ω'_f after 100 ms. The correlation coefficient (r) is 0.89 (0.84) and is highly significant

($p < 0.001$). The regression line which fits the data-points best, has a slope of 7.5/sec (5.8/sec.). From these observations (cf. Figs. 16+17) it seems most likely that the strategy for PAT as applied by the pursuer is a non-predictive⁷ one. This is especially

⁷) Non-predictive means, the pursuer is not able of cutting the intruder's course short during turns, and is constantly lagging behind.

apparent in those phases where the pursuer accelerates to diminish its distance to the intruder (arrows in Fig. 14), however cannot catch it and, instead overshoots directing itself continuously towards the position at which the intruder was some 100 ms before. This is consistent with the earlier findings that mice lacking functional vision are not able to attack an intruder successfully (cf. chapter III.2.2.).

3.2.1.1. Monaural tracking

While directional sensitivity of the visual and the tactile system depends upon retention in the CNS of the neighbourhood relations of the peripheral receptor arrangement (i.e. spatio-topic representation) the directional sensitivity of the auditory system can not be accomplished by reading directly the surface of the peripheral arrangement of receptors, since their location codes for frequency and not for space. Thus directional sensitivity of the acoustic system is assumed to be achieved by considerable central processing i.e. comparing the input of both ears (i.e. of two receptor arrangements). Therefore monaural localization of tone pulses should

not be possible. However mice not only have mobile pinnae, but they were found to exhibit oscillations about the mean tracking trajectory (cf. Fig. 14), thus the prerequisites would be given to apply a successive strategy of monaural sound localization (i.e. by scanning the sound by means of pinna- or head-movements and successively monitoring sound-intensity to obtain the direction of a sound source). In order to investigate, whether or not the mouse is capable of tracking the source of sounds with one ear, mice were fitted with contact lenses and in addition were monaurally deprived. Fig. 18 shows examples of the tracking-performance of such animals (right ear deprived).

The results show, that the intruder's right turns were not successfully tracked and the territory holder ended the pursuit (examples B, C, E). Left turns were slightly too tight (examples A, D). These results strongly contradict the use of a successive acoustic localization strategy. On the other hand, a comparison of the performance of binaurally vs. monaurally tracking mice shows, that for certain values of the error angle

θ_e no significant difference between these two deprivation types can be found (Fig. 19). These

findings indicate, that for error angles greater than about 20° , the acoustic signal perceived by the

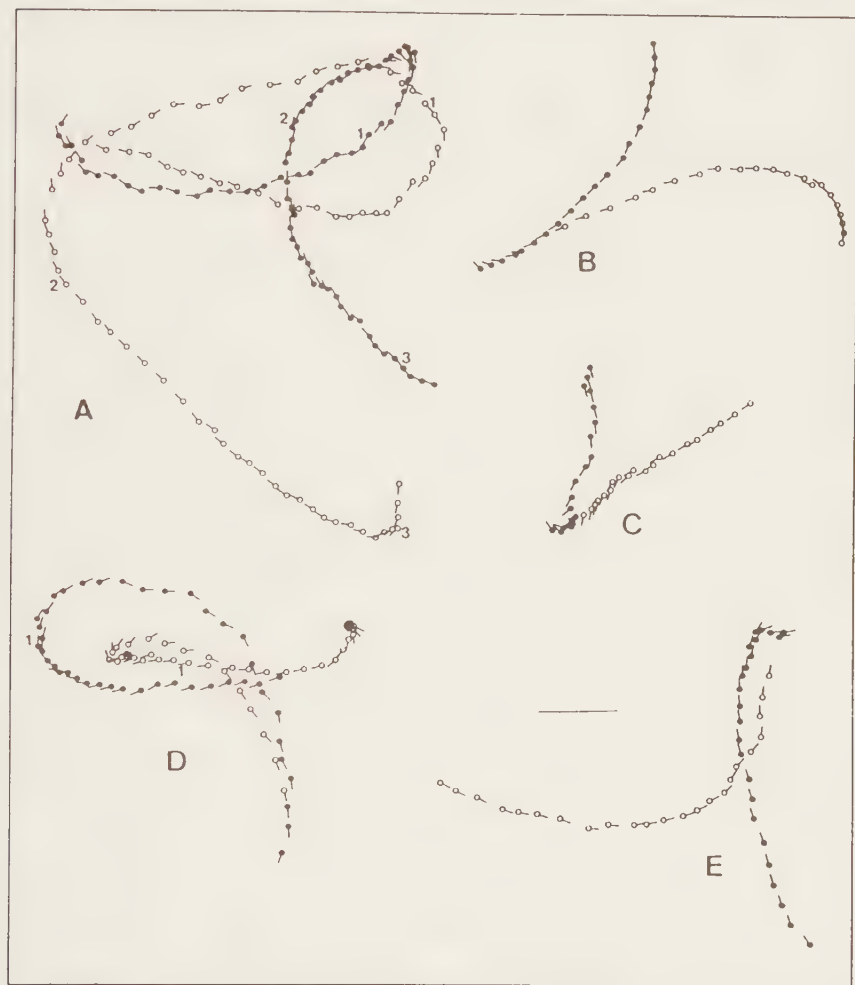


Fig. 18 Examples of tracking trajectories as obtained from mice wearing opaque contact lenses and a silicone rubber ear-plug in the right ear. For explanation of symbols see Fig. 2. (scale = 20cm)

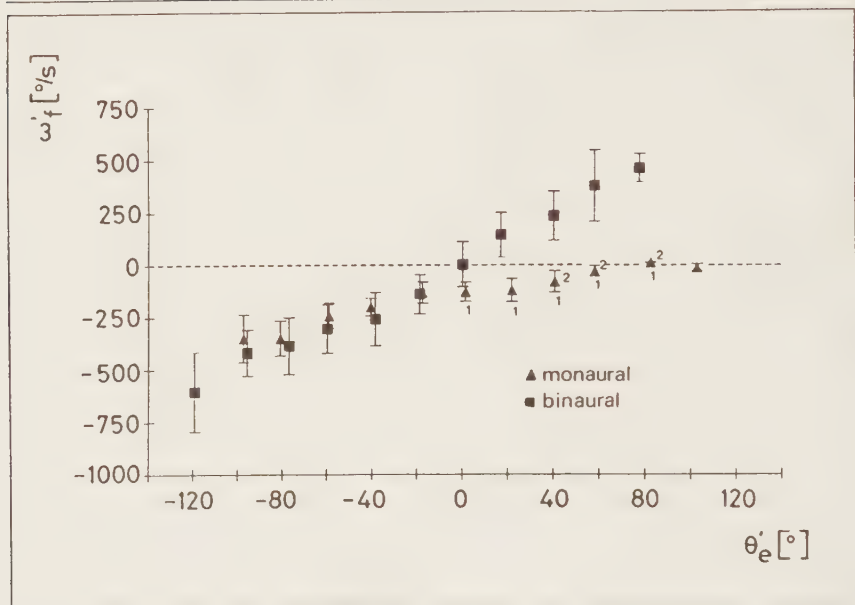


Fig. 19 Relationship between the error angle θ'_e and the angular velocity ω'_f of the tracking animal, for binaural acoustic tracking and for monaural acoustic tracking (with left ear). Data was classified according to θ'_e -values starting at -130° with a class-width of 20° .

error bars represent SEM

- 1 significant difference of ω'_f between the two mouse groups.
- 2 no significant difference of ω'_f from zero.

ear contralateral to the direction of the intruder, is of little consequence for sound localization. Therefore, one can assume that the turning response is triggered predominantly by the ipsilateral ear and therefore the correlation curve should be a function of the mutual spatial characteristics (Richtcharakteristik) of the ear except in a zone of about 40° ,

centered by the animals head axis, where binaural signal processing seems to be necessary for tracking. This finding will be discussed in view of its possible functional implications, since from the literature it is known, that the binocular zone of the visual system in mice is about the same size (DRAEGER and HUBEL, 1975).



Fig. 20 Example of a tracking trajectory as obtained from mice wearing bilateral ear-plugs. For explanation of symbols see Fig. 2 (scale = 20 cm).

3.2.2. Visual tracking

Referencing to Fig. 9, which showed, that in acoustically deprived animals, some tracking behaviour was still persisting, the next step was to investigate the role of vision in tracking. Fig. 20 displays the longest tracking episode which occurred in mice wearing bilateral earplugs.

Unlike acoustically mediated trackings, trackings under visual guidance generally ended either with a "lose" or with a successful attack (i.e. a bite was delivered). When territory holders lost the intruder during tracking, this was obviously due to the limited effective distance of vision (cf. table 5), i.e. as soon as the distance between tracker and intruder surmounted about 20 cm,

tracking ended. Fig. 21 shows an analysis of the tracking displayed in Fig. 20. The same measures as in acoustically mediated trackings were calculated (i.e. the delay time d , and the transposition factor k).

This analysis showed that the delay time in visual tracking (60 ms, cf. Fig. 21 inset a) is shorter than in acoustic tracking (100ms, see Fig. 17 inset a). No statistical analysis can, however, be supplied since the resolution of measurements is as coarse as 40ms. The transposition-factor is slightly increased, (7/sec for visual tracking, vs 5.8/sec, for acoustic tracking). Thus, a correction of the tracking error can be obtained more vigorously and with less delay in visual tracking

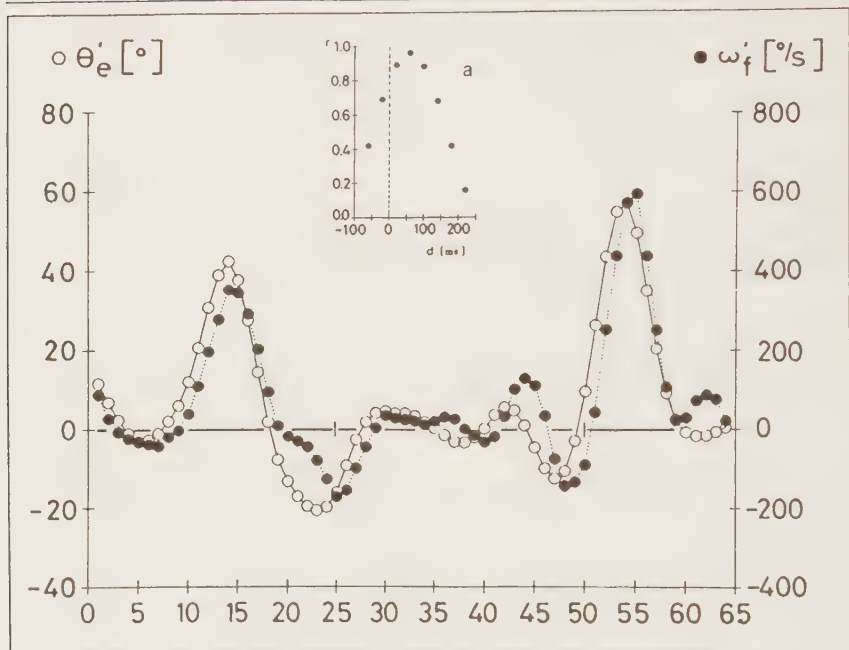


Fig. 21 Relationship between θ'_e and ω'_f during visual tracking as obtained from the tracking in Fig. 20. Inset a: correlation between ω'_f and θ'_e for different intervals of response delay time. The max. correlation occurs at about 60 ms delay time.

as compared to acoustic tracking and as a consequence the former seems to be more accurate than the latter (the maximum correlation between θ'_e and ω'_f was found to be 0.93 for visual tracking vs. 0.84 for acoustic tracking).

3.3. Attacking

While tracking behaviour was found to be remarkably consistent (i.e. performed in a stereotyped manner), attacking behaviour was more variable. Attacking may either ensue at the end of a tracking-phase (becoming evident when the relationship between ω_f and θ_e , as typical for tracking, breaks down) or it may be a straight forward dash

at a stationary intruder. Fig. 22 shows some examples of attacking behaviour. In the former case the territory holder sometimes seems to anticipate the intruder's flight path, i.e. attacking may be predictive (see examples A, B, C, F in Fig. 22). As can be seen from Fig. 23, in a predictive attack

(example B from Fig. 22), there is no clear relationship between θ'_e and ω'_f and the correlation-plot (insert, Fig. 23) reveals independence of the two measures ($r = 0.32, p > 0.05$). While the mechanism underlying these predictive phases remains unknown (possible implications on central



Fig. 22 Examples of attacking behaviour (non deprived animals). Attacks A,B,C and F represent successful attacks, while attacks D and E were unsuccessful. (scale = 20cm).

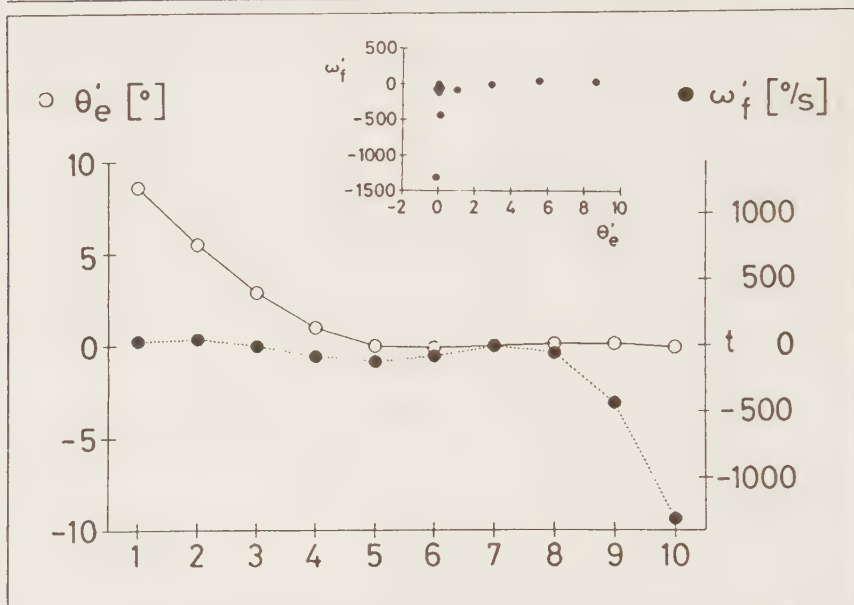


Fig. 23 Plot of error angle θ'_e and angular velocity of the attacking mouse ω'_f as observed during the predictive attack shown in Fig. 22B, not showing the continuous correspondence between the two measures as in acoustic tracking. For explanation of symbols see Fig. 2. Inset: The correlation plot confirms, that no statistically significant correlation is found in this example of predictive attack.

processing will be discussed in section IV.2.2.1), there is good reason to assume, that at least in the very last phase it is an open-loop action (i.e. being performed without stimulus feedback), since a dominant completes its attack even when either the intruder is removed from the path of attack, or when the precalculated collision course misses the intruder, i.e. when the latter initiates a turn at the very last moment be-

fore the attacker has caught up with it (see examples D, E in Fig. 22).

4. Lesion experiments

Lesion experiments were performed in order to gain some knowledge on the neural correlate for passive acoustic tracking (PAT). Thus, all of the following results were obtained from animals wearing contact lenses.

4.1. Lesions placed in the superior colliculus

The behavioural characteristics suggest that PAT is a reflex-like mechanism (i.e. a so-called modal-action-pattern⁸). Since it is known that reflexive movements of eyes, pinnae or head occurring along with a shift of attention are depending on an intact superior colliculus (abbreviation: SC; this brain region is also called mid-brain optic tectum) where multi-modal sensory information seems to converge to generate common motor output (e.g. DRAEGER and HUBEL, 1975); the hypothesis, that the superior colliculus might be involved in guiding the action pattern of PAT, was tested in a series of experiments performed with territory holders in which the S.C. was lesioned. Fig. 24 shows examples of tracking trajectories of mice lesioned either in the left SC (a, N=4) or in both SC (b, N=3). (The histological localizations of these lesions can be found in appendix B).

Territorial mice with lesions in the superior colliculus were clearly not able to track intruders, instead they exhibited excessive ipsiversive circling (unilateral SC-lesioned animals), and instantaneously lost the intruder,

or dashed straight ahead instead of following the intruders' turns (bilateral SC-lesioned animals). That the SC has to be bilaterally intact for successful tracking can also be inferred from the correlation plots presented in Fig. 25. In both cases, unilateral as well as bilateral SC-lesions, no significant correlation between θ'_e and ω'_f can be found ($p>0.05$).

Interestingly however, territory holders with S.C. lesions (either unilaterally or bilaterally) were still able to approach intruders by acoustic cues (see e.g. tracking D in Fig. 24a) as long as they remained stationary or moved only slowly.

⁸) In an attempt to define the units of behaviour, LORENZ and TINBERGEN (LORENZ, 1932) argued, that each species had a repertoire of so called "Erbkoordinationen", which were supposed to be a diagnostic feature of that species as much as e.g. morphological characters. The concept of the "Erbkoordination" however entered the English literature somewhat mistranslated as "Fixed Action Patterns" (FAPs). However in closer analysis many of these FAPs turned out to be not as fixed as assumed at all, therefore BARLOW (1968) suggested the use of the alternative expression "Modal Action Pattern" (MAP) which is used in this work to name a stereotyped, highly predictive, species specific behaviour sequence.

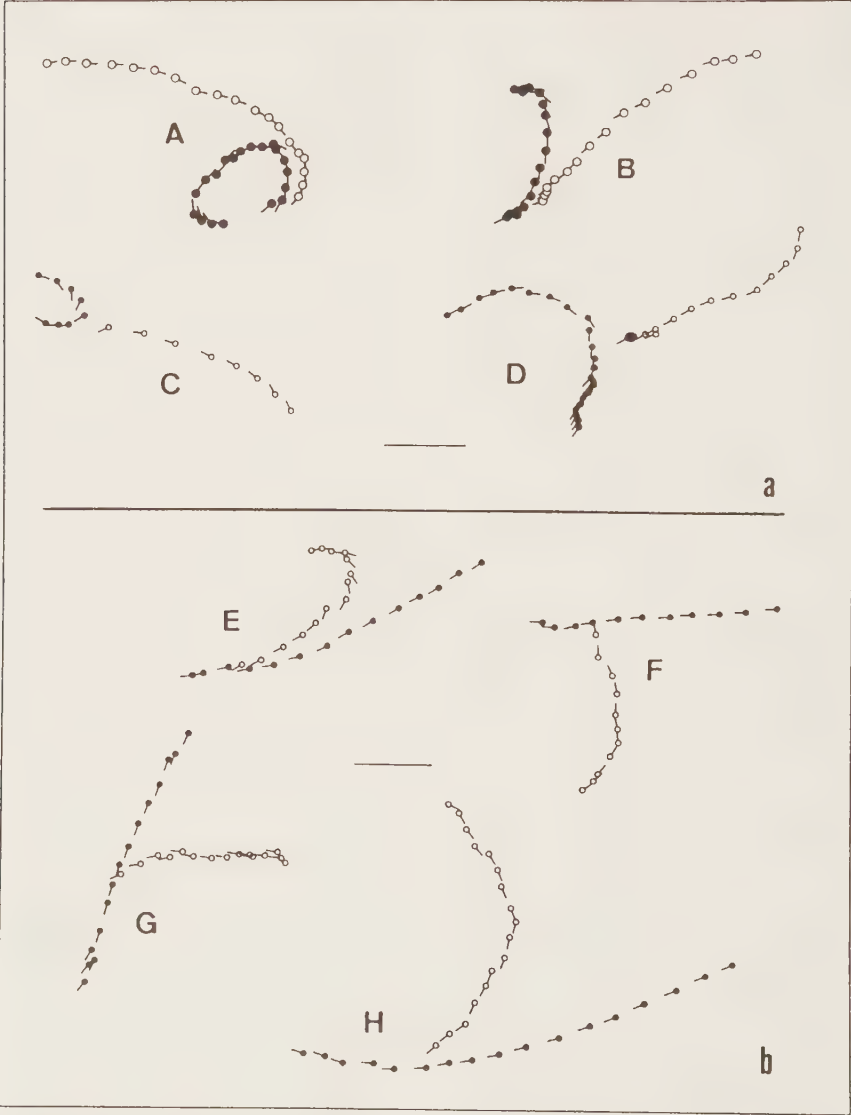


Fig. 24 Examples of PAT trajectories, as obtained from mice lesioned in the left SC (a), or lesioned bilaterally (b). Further explanations see text (scale = 20cm).

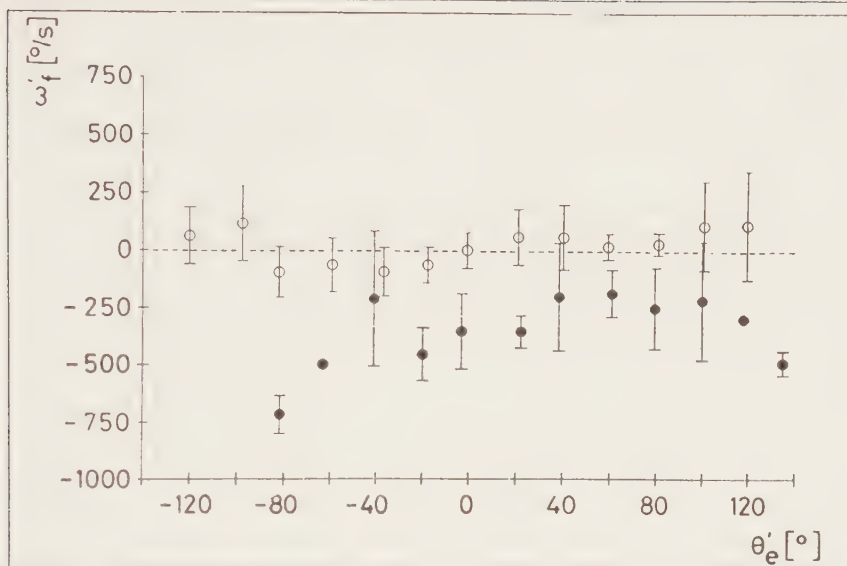


Fig. 25 Relationship between θ'_e and ω'_f in both, unilaterally (○) and bilaterally (●) SC-lesioned animals.

4.2. Control lesions

A few lesions were performed in various parts of the brain, i.e. hippocampus and cortex (N=4) and also unilaterally in the medial geniculate nucleus (MGN) (N=3, localization of lesions see appendix B), which is known to be an important acoustic relay station to the cortex. As can be seen from Fig. 26, as opposed to SC-lesions, all these control lesions (including those in the MGN) left PAT intact (no significant difference to controls without lesions was found, considering the cor-

relation between θ'_e and ω'_f ($p > 0.05$, X^2 -test). Thus the geniculo-cortical pathway of audition does not seem to play an important role in acoustic tracking. This finding, together with the above result, indicating that SC-lesioned animals could still effectively approach intruders will be considered in section 5 of the discussion, in view of a hypothesis that assumes two parallel neural channels in the mouse acoustic system serving different behavioural functions.

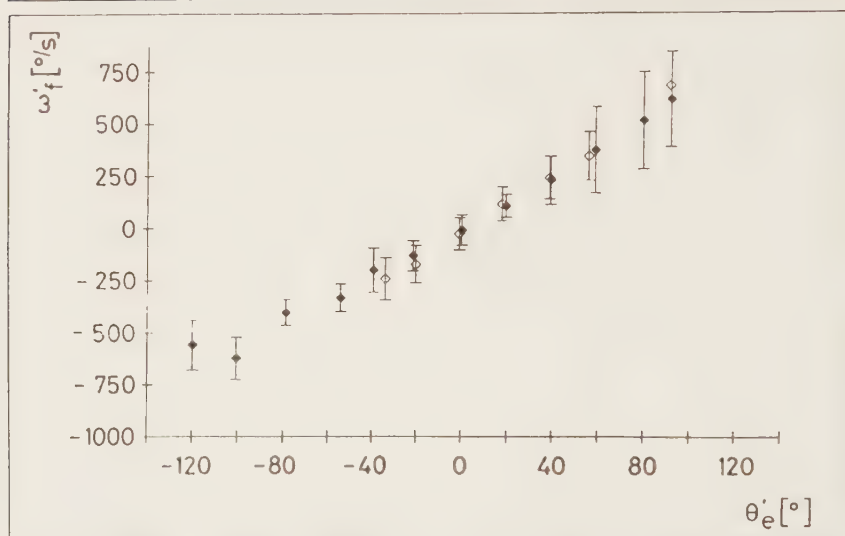


Fig. 26 Relationship between the error angle θ'_e and the angular velocity of the tracking animal ω'_f as found in animals receiving control lesions in various parts of the brain, i.e. cortex or hippocampus (♦) and MGN (◇). No difference was found as compared with acoustic tracking of controls, cf. Fig. 19.

PART B. ANALYSIS OF AGONISTIC BEHAVIOUR IN CAGES

Some aspects of mouse aggressive behaviour, especially those related to interactions of close proximity, are preferably analysed under cage conditions, where interactions occur very frequently and can readily be observed and evaluated. Although it is well realized that cage encounters of the type reported here are complex interactive entities, where the behavioural acts of the two opponents are heavily interdependent, the basic conditions are the same for control- and for test-residents and thus an evaluation of the residents' behavioural data can provide reliable results, without further analysing the intruder's actions. In this part of the results' chapter, the role of some of the mouse's sensory modalities (audition, vision, olfaction, tactile sense) in aggressive behaviour in cages is investigated.

1. The development of cage aggressive behaviour (CAB)

The aim of this experiment was

to investigate the development of aggressive behaviour in isolated mice (cage residents) during subsequent trainings (cf. section II.2.2.1). The result is depicted in Fig. 27. As can be seen, there was a remarkable increase in offensive behaviour OFF (for elements see category OFF in table 4) and in ambivalent behaviour AMB (categories: OFA and DIA) from the first to the second training. A less pronounced increase could be found in non-social behaviour NSO (category: non-social behaviour in table 4), while in the categories SOX (in table 4, categories: SAT, SCO and SEX) FLI (categories: ARF, DEA and ESC) a clear decrease was seen, during subsequent trainings. Thus, although offensive behaviour and ambivalence behaviour tended to reach a plateau the other behavioural categories did not seem to stabilize within these three trainings. As a consequence, aggressive mice to be deprived of a sensory modality for the following experiments could not serve as their own controls, but had to be matched with an equal number of aggressive cage residents remaining undeprived, serving as controls.

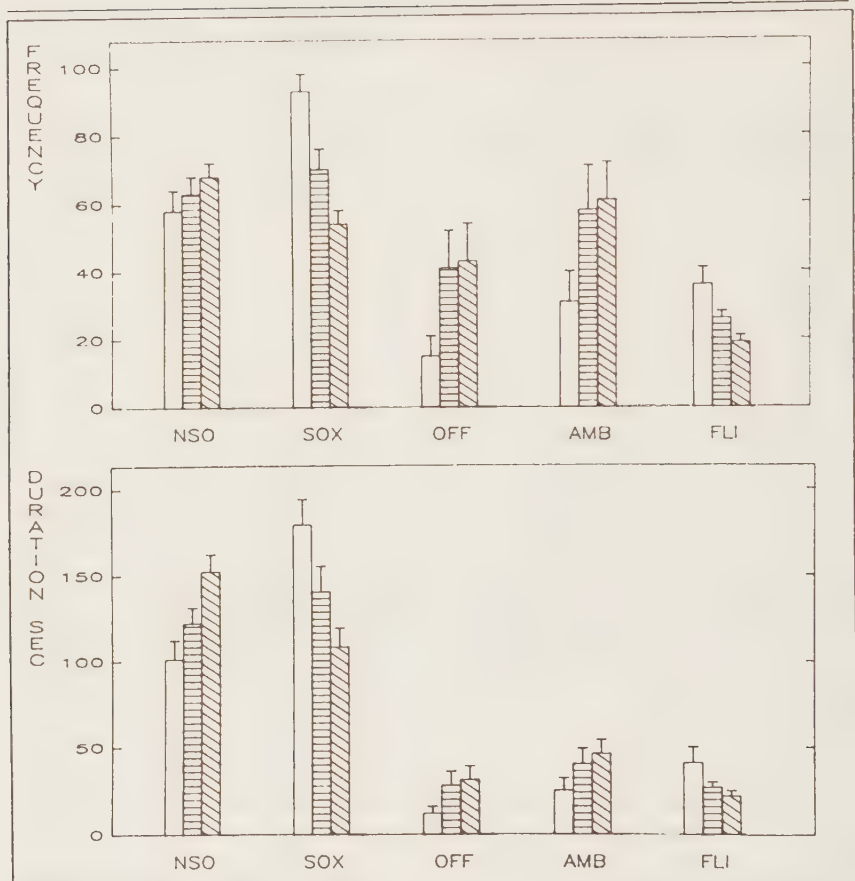


Fig. 27 Effects of repeated training on consecutive days, on the aggressive response of isolated mice. Bars represent mean-values and error-bars the corresponding SEM ($N_{\text{animals}}=14$). Plain bars: 1st training, horizontally hatched bars: 2nd training, left-hatched bars: 3rd training. Further details and commentary are given in the text.

2. Time analysis of cage aggressive behaviour

The 6 min. observation period used in all cage experiments has

been chosen somewhat arbitrarily. However, it was supposed to provide a good representation of cage aggressive behaviour (DI-

XON, personal communication). Since a change of the overall structure of agonistic responses occurring during this observation period could not have been discounted a time analysis was performed, i.e. the 6min. observation time was split into six 1-min intervals which were evaluated separately. Fig. 28 shows this minute by minute sequenced behaviour of isolated cage residents. As can be seen, there was a reasonable evenness in the distribution of the different observed behavioural categories

over the 6 single-minute observation intervals, i.e. the structure of aggressive behaviour as displayed by cage resident animals towards intruders remained constant throughout the observation period (the X^2 -test revealed no statistically significant deviation from a uniform distribution, $p>0.05$). Thus the used experimental paradigm seems to be suited for the following analysis.

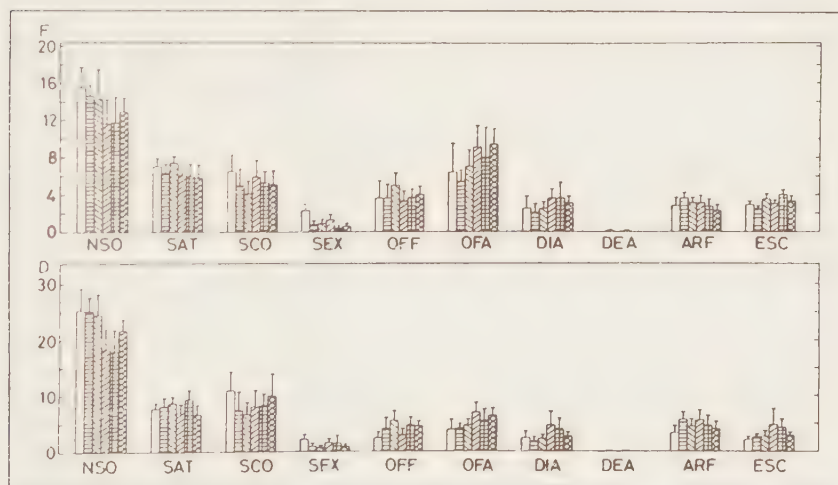


Fig. 28 Single minute time analysis of the 6 min. observation period. Abbreviations: NSO=non-social behaviour; SAT=social attention; SCO=social contact; SEX=sex-related behaviour; OFF=offensive behaviour; OFA=offensive ambivalence; DIA=distance ambivalence; DEA=defensive ambivalence; ARF=arrested flight; ESC=escape (cf. Table 4). Commentary see text.

3. The effects of sensory deprivation on cage aggressive behaviour (CAB)

Analysis of CAB was done on the basis of the mouse ethogram displayed in table 4. While the results of deprivation-experiments in cages will generally be presented in terms of categories (not single elements), raw data can be found in appendix A. Statistic measures in all experiments refer to the Mann-Whitney U-test, unless explicitly stated otherwise.

3.1. Effects of olfactory deprivation on CAB

From the literature it is well known that olfactory cues associated with male urine play a crucial role in intermale aggressive behaviour (e.g. ROPARTZ, 1968b; MUGFORD and NOWELL, 1970), and recently two substances have been identified (DEHYDRO-exo-BREVICOMIN, 2-sec-BUTYL DIHYDROTHIAZOLE) which bestow aggression inducing properties to water, similar to that observed with male urine (NOVOTNY, et al, 1985). Furthermore, we have seen, that territorial animals with combined acoustic and visual deprivation still seemed to be

aroused after introducing intruders into their territories, suggesting that olfactory cues may be responsible for arousal. Therefore, the first interest laid on an inspection of the effects of olfactory deprivation on CAB. Depriva-

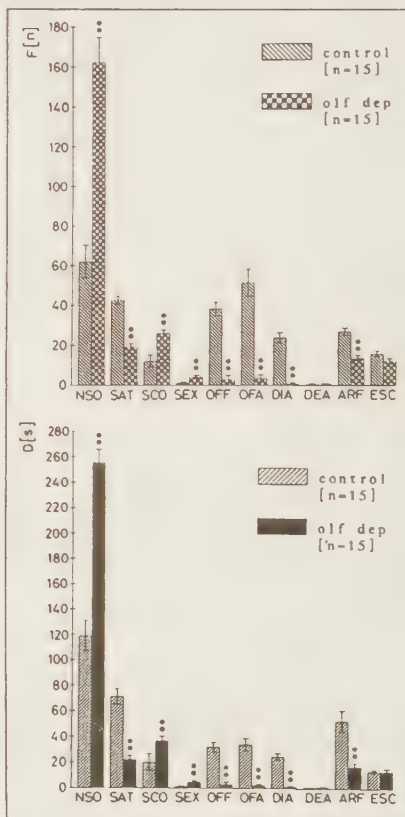


Fig. 29 CAB as displayed by ZnSO_4 -treated mice 1 day after deprivation. For explanation of abbreviations and statistics, see Fig. 28. Commentary see text.

vation was effected by the Zn-SO₄-method. The results are depicted in Fig. 29.

It was found, that elements of behaviour belonging to the categories OFFense (OFF), OFFensive- and DIstance- Ambivalence (OFA, DIA) were almost completely absent in these animals. A further analysis of the data (not presented) showed, that a small remainder of agonistic behaviour was not evenly distributed over all of the deprived animals but was attributed to 3 out of the 15 animals, which were most likely not fully olfactory deprived (cf. discussion/histology, section IV.5.1.). In addition, aggressive elements displayed by these 3 animals occurred only at the very end of the observation period, i.e. during the last 30 sec. Non-social behaviour was heavily increased showing that the deprived animals were not generally depressed in their behaviour. The increased value for non-social behaviour may be interpreted as non-specific behavioural activation. The decreased value for Social ATtention (SAT) suggests the same, while the increased value for Social COntact (SCO) is probably indicative for the the resident's urge

to "identify" the opponent. Towards the same end points the significant increase in SEX-related behaviour (SEX) which was mainly due to the higher value obtained for the element "follow" (cf. appendix A).

3.1.1. Restoration of aggressive behaviour after olfactory deprivation

Since ZnSO₄-treatment acts mainly on peripheral parts of the olfactory mucosa, leaving most of the underlying tissue, which provides the substrate for regeneration of olfactory cells, intact (MATULIONIS, 1975), this deprivation is mutually reversible (see however discussion of this point in section IV.5.1.). We therefore retested the treated animals along with controls 4 and 20 days after deprivation. Figs. 30 and 31 show the results. 4 days after deprivation, some changes in behaviour became overt (Fig. 30). Non-social behaviour of the test animals was still significantly higher than in the controls, however there was a trend toward a smaller difference to the control value. Social contact was again increased. OFF showed a very slight increase as compared to day 1 testing,

being however still highly significantly reduced, compared to controls. A detailed analysis showed, that in this test-group 5 animals (out of 15, cf. 3.1.)

displayed elements of offensive or offensive ambivalent behaviour as compared with 3 animals in day-one test. Sexual behaviour showed again a significant

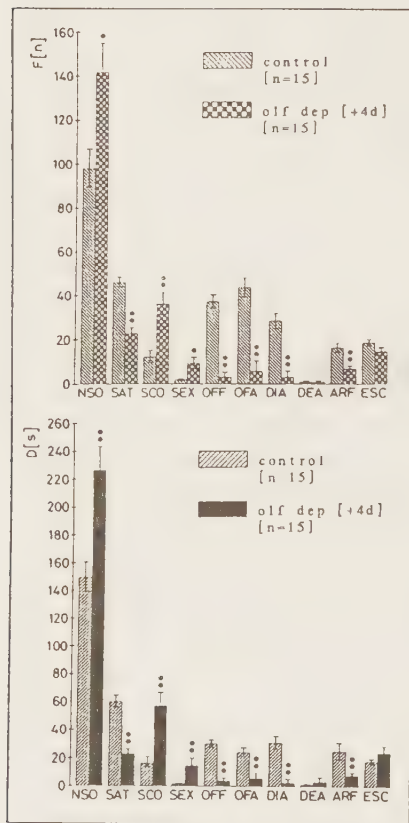


Fig. 30 Restoration of CAB in ZnSO_4 -treated mice 4 days after olfactory deprivation. For explanation of abbreviations and statistics, see Fig. 28. Commentary is given in the text.

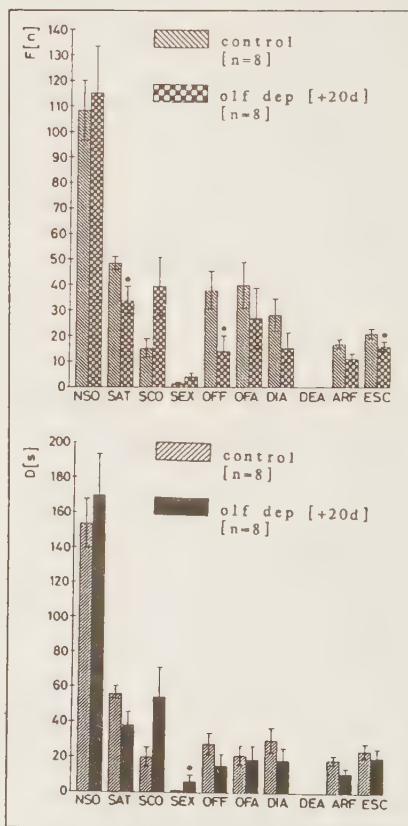


Fig. 31 Restoration of CAB in ZnSO_4 -treated mice 20 days after olfactory deprivation. For explanation of abbreviations and statistics, see Fig. 28. Commentary is given in the text.

increase, due to an increased level of elements clearly attributable to mating, i.e. "attempted-mount" and "mount". The reason for this phenomenon remains unclear, but possible implications will be discussed in section IV. 2.1.

Twenty days after deprivation, the picture had changed considerably whereby frequency as well as duration of the various behavioural elements of test animals, as compared to controls, showed a consistent trend towards normalization (Fig. 31). Thus non-social behaviour occurred equally frequently in the two experimental groups. (Due to the greater inter-test interval, the baseline level of non-social behaviour had also increased.) SAT and OFF differed between deprived animals and controls in terms of frequency but not in duration and OFA and DIA were no longer significantly different. A detailed analysis revealed, that 20 days after deprivation, 6/8 of the treated mice showed elements of aggressive behaviour (the corresponding value for control animals being 8/8). SCO was still increased, although (because of the great variance between the

test animals' responses) not reaching significance.

3.1.2. The histological analysis of the effects induced by ZnSO_4

The results obtained in the last section suggested, that the normal structure of aggressive behaviour in cages as displayed by the cage-resident seems to be regained, some time after ZnSO_4 -induced coagulation of the olfactory mucosa. Consequently, regeneration capabilities of the aggression-mediating system (i.e. olfaction), must be assumed. Whether the behavioural findings are correlated with histological changes in the olfactory mucosa was therefore questioned next. Fig. 32 shows typical photographs of the olfactory mucosa under control conditions and at various intervals after deprivation. Interestingly, on day 1 after treatment, no pathological changes could be observed. On day 6- and day 13-preparations the olfactory epithelium(E) was disorganized and much reduced in thickness. There was fusion of cells with loss of cilia. The cells appeared cuboidal rather than tall columnar. Cell necrosis characterized by pyknosis, va-

cuolization and infiltration by neutrophils was seen. In the lamina propria, the tubulo-alveolar glands had excessive secretion and there was exfoliation of cells and exudation of proteinaceous material in the nasal cavities. Mild nerve fiber degeneration was also seen. On day 13 in addition, mild to moderate vasculitis and perivasculitis could also be seen. On day 20 and more especially on day 26 the olfactory epithelium was still reduced in thickness and

stunted but squamous metaplasia of the epithelium and some hypertrophy of the tubulo-alveolar glands could be seen, which may indicate the initiation of the regenerative process.

3.2. Effects of acoustic deprivation on CAB

From the results of the enclosure experiments (see part A.2.1.), audition appeared to be the sensory modality predominantly engaged in the evaluation of distant cues, i.e. for "attend"

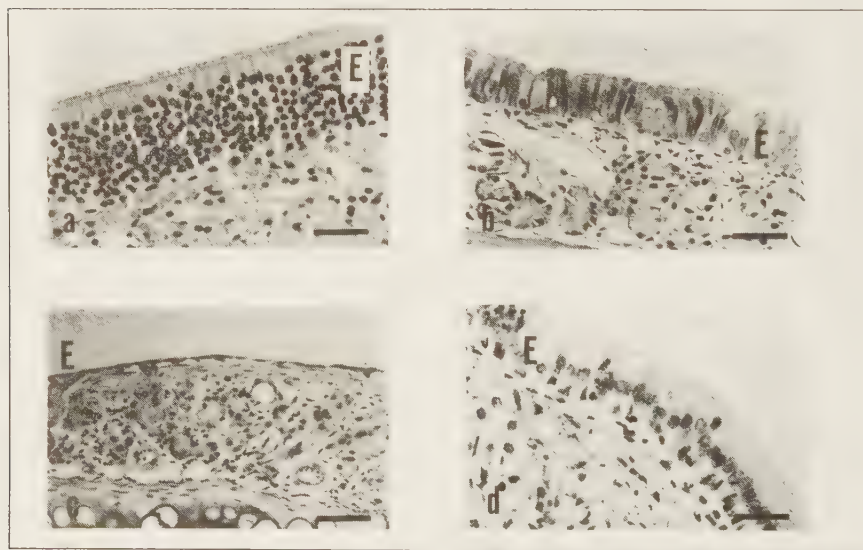


Fig. 32 Histological analysis of the olfactory mucosa under control conditions (a) and at various intervals after deprivation (b=6d; c=13d; d=26d), showing degeneration of olfactory mucosa and partly of underlying tissue and beginning regeneration (day 26). Scale = 1mm). E=epithel. For further explanation see text.

and "approach" and in "tracking". Since in cages, the distance between the two opponents is generally smaller during aggressive encounters (i.e. in the range of 0-30 cm and thus often within the effective distance of

vision) cage aggressive behaviour would not be expected to be drastically influenced by acoustic deprivation. And indeed the results represented in Fig. 33 attest just this.

A certain increase in NSO behaviour (significant only in terms of duration) could be observed whereas SAT (being related to "attend" in enclosures) was significantly reduced. However this reduction in SAT was not as clear in cages as in enclosure-experiments, which is readily explained by the generally shorter distance between the two opponents, i.e. vision can be made responsible for most of the remaining SAT-behaviour. In all other categories no differences between test- and control-animals were found, although SCO showed a trend toward reduction. Thus, these results perfectly parallel those obtained in enclosures.

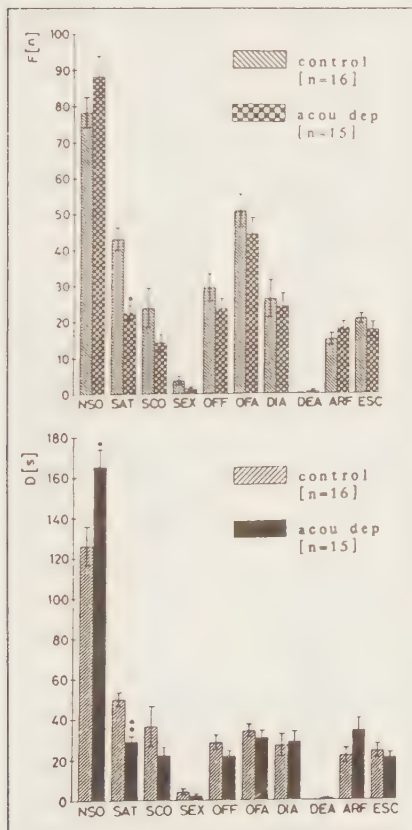


Fig. 33 Effects of acoustic deprivation on cage aggressive behaviour (CAB). Explanation of abbreviations see Fig. 28. Commentary see text.

3.3. Effects of visual deprivation on CAB

Vision had been shown in the enclosure experiments to be important mainly for attacking behaviour (chapter III.A.2.2.). Attacking-behaviour, as seen in enclosures is not analogous to

the element "attack" in cages, since due to limited space, the intruders' flight response to the resident's aggression is predominantly of the static type, i.e. ARF, while during attacking behaviour in enclosures intruders mostly display escape elements. Nonetheless, visual deprivation in cages can be expected to have a distinct influence on the occurrence of various behavioural elements associated with attacking and biting the intruder. The results, showing this, are depicted in Fig. 34. SAT was reduced in frequency illustrating the relative role of vision for "attending" behaviour at close quarters. The behavioural category of OFF (which contains the elements, "threat", "attack", "bite", "chase" and "aggressive groom"), seems not to be affected quantitatively by visual deprivation. However, a closer look clearly shows, that a qualitative change had taken place. Thus, bites delivered by a deprived cage-resident were very often straight ahead, right into the face or towards the belly of the intruder, which was very rarely seen in undeprived cage residents. The latter commonly displayed an "offensive side-

ways posture" before placing a bite. This more direct offensive behaviour and reduced ambivalence in visually deprived animals, becomes evident considering the significant decrease in the categories of "offensive

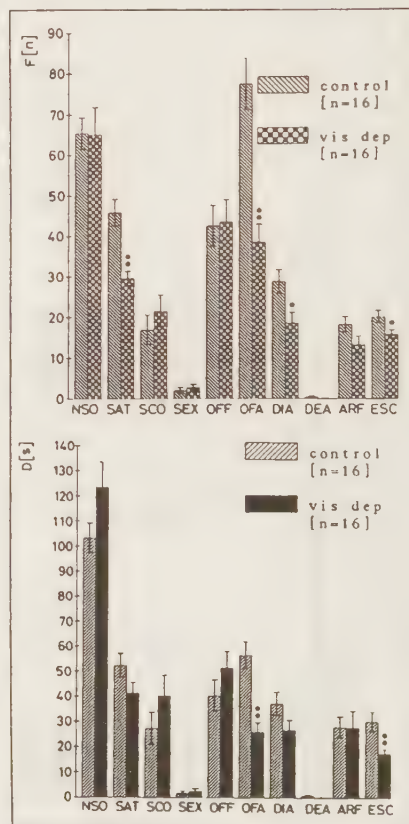


Fig. 34 Effects of visual deprivation on CAB. Explanation of abbreviations see Fig. 28. Commentary in text.

ambivalence" and "distance ambivalence" as compared to undeprieved aggressive animals. Two consequences can be drawn from these findings: Firstly, visual cues emerging from the cage intruder animal seem to induce ambivalence in the aggressive animal (cage resident). Secondly, since the frequency of bites is not reduced in visually deprived mice, another sensory modality than vision must take over the guiding of the bite towards the intruder mouse.

3.4. Effects of vibrissal deprivation on CAB

The above results raise the question as to how a visually deprived aggressive mouse can properly aim its bites towards a stationary intruder. Closer inspection of visually deprived aggressive animals' behaviour shows, that the offensive sideways posture adopted by the aggressive animal when placing a bite, brings the aggressors vibrissae in contact with the intruder. Thus if the function of the vibrissae is to aim the bites at the intruder, delivery of bites by vibrissally deprived animals should severely be hampered. Fig. 35 shows the results, con-

firming this expectation.

Not only is OFF-behaviour significantly reduced (due mainly to decreased bites, see appendix A), but ambivalent behaviour is highly increased. The most pronounced effect is seen in the

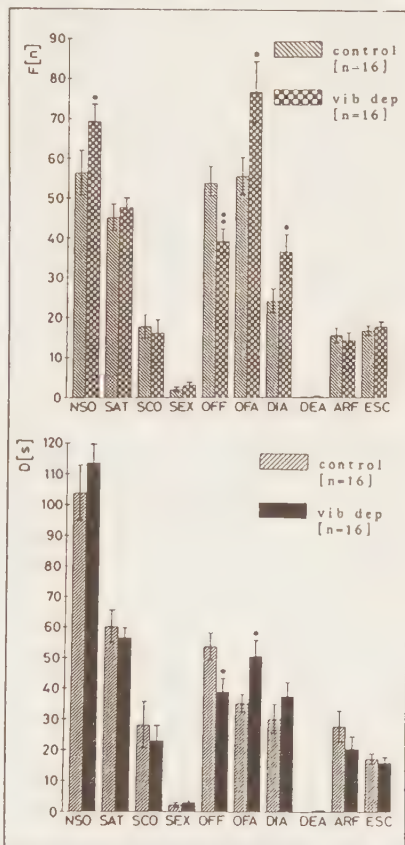


Fig. 35 Effects of vibrissal deprivation on CAB. Explanation of abbreviations see Fig. 28. Commentary in text.

category of OFA, where a massive increase in the elements "parry" and "offensive sideways posture" probably document the deprived cage-resident's tendency to replace the tactile input normally provided by the vibrissae, by tactile input gathered by tapping with the forepaws. DIA is increased, mainly due to the increase in the frequency of the element "rattle". This latter finding may be interpreted in this context as displacement activity, resulting from the impaired successfulness to bite the intruder. The results thus show, that the ultimate direction of bites is performed by means of tactile cues and a comparison of these results with the ones obtained with visually deprived cage residents (see section 3.3), suggests a functional interplay between tactile and visual input in cage aggressive behaviour.

3.5. Effects of combined visual and vibrissal deprivation on CAB

The results described in sections 3.3 and 3.4 show, that some of the effects caused by visual deprivation were opposed to those of vibrissal deprivation (i.e. in the categories OFF and OFA

as well as DIA). Thus, the experiment to be described was designed to find out, whether in animals undergoing combined deprivation, the changes induced by visual deprivation would

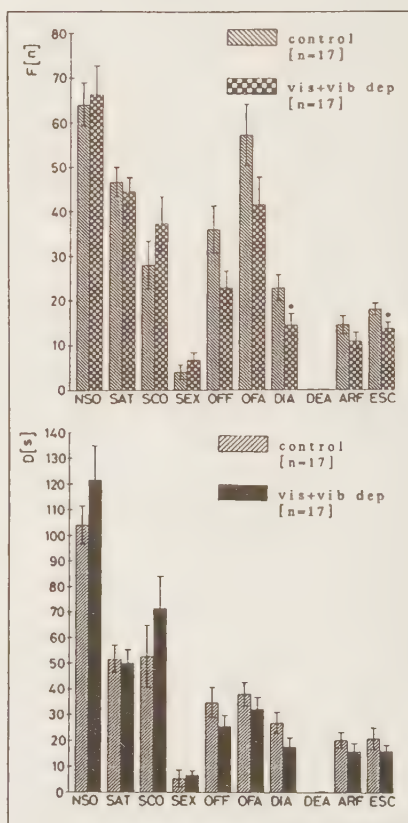


Fig. 36 Effects of combined visual and vibrissal deprivation on CAB. Explanation of abbreviations see Fig. 28. Commentary in text.

override those induced by vibrissal deprivation, or vice versa correspondingly. The results presented in Fig. 36 show, that the frequency of OFF in animals with combined deprivation was reduced (although not reaching significance) as during vibrissal deprivation, while DIA followed the corresponding findings in visually deprived animals (i.e. was also significantly reduced, $p < 0.05$). OFA was reduced in aggressive cage residents as well (although not reaching signifi-

cance). This latter finding may however be a secondary effect, simply reflecting the decreased frequency of OFF-behaviour. To obtain a more reliable measure, an OC (offense coefficient) was devised, to demonstrate the cage resident's tendency to behave aggressively toward the intruder. The OC expresses the amount of offence relative to offensive ambivalence in test animals as compared to controls, according to the following formula⁹:

The values of OC, obtained from animals with either visual, vibrissal or combined deprivation

$$OC = [OFF(fD)/OFA(fD)]/[OFF(fK)/OFA(fK)]^9$$

are given in table 6.

	visual deprivation	vibrissal deprivation	visual + vibrissal deprivation
OFFENSE COEFFICIENT	0.49	1.90	1.15

Table 6 Offense coefficient [OC] for the various deprivation types as calculated to analyse the interaction of the visual and tactile sense in CAB. Commentary see text.

⁹) OFF(fD) e.g. means the frequency of OFF-elements as displayed by the deprived animal. An OC of 1 would mean, that the relation between straightforward OFF and OFA is the same in controls as in deprived animals, whereas values < 1 mean, that the deprived animals are biased toward OFF and values > 1 that the deprived animals tend to behave more ambivalently.

It can be concluded from the OC's above, that some form of compensation between visual and vibrissal input indeed takes place, during cage aggressive behaviour and this again stresses the close interplay between these two senses during a certain stage of the cage resident's aggressive response toward the intruder.

IV. DISCUSSION

1. The structure of mouse agonistic behaviour

Ethological studies have revealed that behaviour has a structure in which different acts and postures, collectively known as elements, occur in sequences which are related to each other in a characteristic manner. These elements form the units of observable behaviour. The results of this study show, that close observation of aggressive encounters between mice in territories or cages allow the behaviour to be broken up into main subunits, on the basis of single or grouped distinct motor patterns. The succession and appearance of some of these subunits is however clearly depending on the situation (e.g. space available). This is illustrated in Fig. 37, which brings a general model of mouse aggressive behaviour. Thus, in enclosures as well as in cages, the first change in the territorial- or cage resident animal's behaviour is seen as increased arousal, and almost

certainly a change in motivation (i.e. interpreted from the animal's increased likelihood of showing aggressive episodes). Cages (due to limited space available), with intruder animals displaying the static postures of arrested flight [ARF]), generally predispose to more static types of aggressive elements, whereas in enclosures (where the intruders typically escape from the aggressive animal) dynamic acts of aggression predominate. The static type of aggression is not only preceded but also accompanied by behavioural elements belonging to the category of offensive ambivalence (OFA) and all other categories as shown in the ethogram in table 4. In the present study, behaviour was measured in terms of ethological elements, classified according to the usual morphological criteria as described by GRANT and MACKINTOSH (1963) or DIXON (1986). However, as shown in the next section, the present study provides a basis for re-classification of certain aspects of the mouse ethogram according to sensory-physiological and neuroethological criteria. Despite the extensive ethograms available, and although aggression has been the

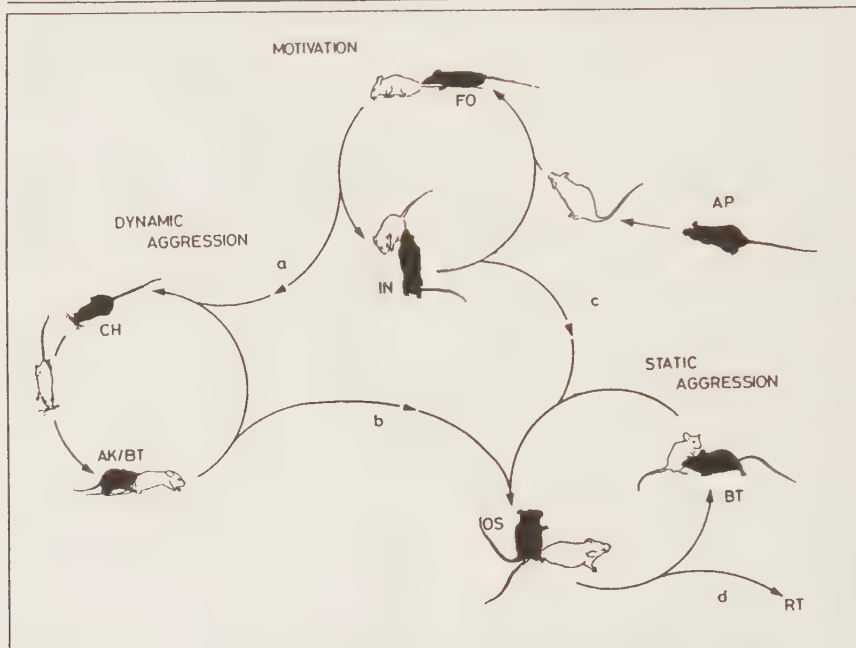


Fig. 37 Model for intermale aggressive behaviour in mice. After detecting and approaching an intruder, the territorial animal displays elements of social contact, e.g. follow, investigate and subsequently is motivated to behave aggressively, i.e. showing the dynamic type of aggression (a) or the static type of aggression (c), depending on escape space available for the opponent animal.

Elements: AK = attack, AP = approach, BT = bite, CH = chase, FO = follow, IN = investigate, OS = offensive sideways posture, RT = retreat. (For further explanations see text).

principal focus of experimental attention, an analysis of the specific motor patterns of mouse aggressive behaviour under semi-natural conditions has received little attention. The present results show that once the territorial animal is motivated

to behave aggressively, dynamic aggression is not accompanied by other approach related behavioural elements but appears to consist of 4 phases: 1. detection/localization, 2. approaching, 3. tracking (=chasing), 4. attacking. Thus it is suggested, that the

present definition of elements and the arrangement in the above phases may serve as guideline for further studies. Similarly GRIF-FIN, WEBSTER and MICHAEL (1960) could distinguish among three phases of insect hunting behaviour by myotis lucifugus and ptesicus fuscus, i.e: 1. search phase, 2. approach phase, 3. terminal phase, each characterised by a different sonar signal type. Another example would be structuring of visual prey catching of the frog rana pipiens, into the three phases: 1. orienting, 2. approaching, 3. snapping. Each of these phases being characterised in terms of the corresponding releasing stimuli, i.e. size, shape and distance of objects (GROB-STEIN et.al., 1985). As a consequence, the macrosystem of mouse agonistic behaviour seems to provide a further excellent model to study a highly integrative behavioural process by way of breaking it up into different subsystems.

2. The sensory control of aggressive behaviour and its phases

The results presented in chapter III.A.2. show, that selective deprivation of the various senses

exerts profound impairment of phases of territorial behaviour, albeit to differing degrees. Although, it is realized (and will be discussed in the following sections) that at certain points of the response sequence, interactions between these senses may occur, generally a specific sensory modality predominates, suggesting that the specified main phases are not merely arbitrary but represent physiologically distinct, albeit functionally related events. Thus territorial aggressive behavioural acts involve frequent modality switching. Since animals as diverse as fishes, rodents, anurans or birds, all face a number of common problems in terms of sensory-analysis of their "umwelt" used for the coordination and direction of behaviour, (for reviews see e.g. POPPER and FAY, 1980; FINLAY and SENGELAUB, 1981; COLLETT, 1983) appreciation of common functions may point the way toward the discovery of analogous or even homologous mechanisms or neural units within vertebrate sensory systems. Thus in this chapter, the results of the present study and their implications are discussed in the light of comparative sensory physiology.

2.1. Motivation¹⁰ for aggressive behaviour (olfaction)

Since agonistic behaviour is only one aspect of mouse behaviour, the start of any social interaction should involve a mechanism which is sophisticated enough to allow a certain sensory-motor-interfacing mechanism to be activated, i.e. a flexible and adapted response towards a conspecific. Thus a female i.e. potential mate should be treated differently from a potential competitor. In the latter case a selective release of agonistic motor patterns, suited to expel a conspecific out of a territory or to attack it, is indicated. The systematic studies reported here, relating specific sensory stimuli to the release and modulation of agonistic behaviour, show that although each of the visual-, acoustic- and somatic- senses is important, neither of them alone, is critical i.e. would prevent the dominants from displaying aggressive behaviour upon its deprivation (not even in case of combined deprivation of all of them, cf. Fig. 38. Under cage-conditions, where withdrawal of the intruder is limited, offense-behaviour of the resident is not reduced, compared to controls.

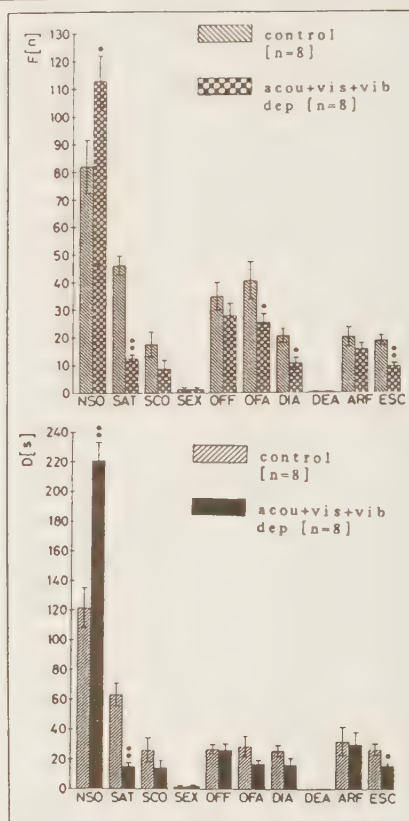


Fig. 38 Effects of combined acoustic-, visual- and vibrissal deprivation on cage aggressive behaviour. Explanation of abbreviations see Fig. 28. Commentary in text.

¹⁰⁾ Motivation as it is understood here, means any internal, yet unidentified mechanism, that leads to the display of aggressive behaviour in the analysed animal.

While in enclosures, deprived animals' aggression is reduced. Of interest is, that in both situations, the non-social behaviour of deprived animals (i.e. NSO in cages, lok in enclosures) is markedly increased. These facts suggest the following: a) Increase in non-social behaviour and/or exploration represents active searching by the deprived animal for aggression releasing cues, i.e. exploration may in this case represent aggressive motivation. b) The fact that aggression subsides in enclosures but not in cages almost certainly refers to dependence on olfactory cues. These operate at close quarters and are the main stimuli triggering the isolated animals' aggression.

The latter conclusion is supported by many observations found in the literature, although most of the evidence is somewhat indirect, being obtained, using the strategy of defining or manipulating olfactory cues (i.e. method type a, cf. II.2.), such as applying strange animal urine to the fur of one of two familiar cage inhabitants, and reporting altered behaviour. Thus it has long been known, that individual recognition is achieved by olfaction

(BOWERS & ALEXANDER, 1967; KALKOWSKI, 1967). MACKINTOSH and GRANT (1966) could demonstrate the aggression eliciting properties of strange male odour associated with urine. MUGFORD and NOWELL (1970) additionally showed, that the potency of aggression releasing properties of male urine is correlated with the social status of the corresponding mouse. DIXON and MACKINTOSH extended these results in that they found, that female urine (taken from adult [1971] as well as juvenile [1976] animals) has an inhibitory influence on male aggression and that this effect is not dependent on the female's oestrous state (1975). "Offense" is furthermore usually preceded and accompanied by investigation of the opponent's body (LEHMAN and ADAMS, 1977).

While the above types of experiments have demonstrated, that alteration in the quality of olfactory stimuli modify agonistic behaviour, little work has been carried out at the receptor level, i.e. manipulation of the sense organs itself in the mouse. It was shown, that bilateral ablation of olfactory bulbs completely abolishes aggression in mice (RO-

PARTZ, 1968). However caution is necessary in interpreting such results, since bulbectomy also exerts great non-specific effects on behaviour (WENZEL and SALZMANN, 1968) and alters many neurotransmitter titers in the brain (CAIRNCROSS, et.al., 1978; HIRSCH, 1980). BRAIN et.al (1982a) have used the more peripherally acting deprivation-technique of flushing the olfactory mucosa with ZnSO_4 , using the method of ALBERTS and GALEF (1971). They found, that acute ZNSO_4 -anosmia removed fighting in 9 out of 11 treated animals, while chronic treatment lead to 0 animals fighting out of 10 tested. Some uncertainty however lingers with these experiments, since chronically treated mice showed a significant loss in body weight (some animals even died), probably indicative of toxic effects of ZNSO_4 swallowed by the animals during application. Our study clearly shows, that peripheral anosmia inflicted by ZnSO_4 blocked aggressive behaviour thus confirming the necessity of olfactory stimuli. Paradoxically however, the drastic behavioural changes on days 1 and 4 were not directly correlated

with the biological changes observed. This interesting finding remains to be explained. Nevertheless our results are compatible with those obtained by BRAIN et.al., i.e. "offense" and "offensive ambivalence" were almost completely abolished in "olf-dep"-animals.

Furthermore, the results indicate a correlation between beginning regeneration of the olfactory mucosa and reappearance of "offensive behaviour" 20 days after deprivation was effected. Remarkably enough however, while regaining aggression, some isolated residents showed overt sexual behaviour (especially pronounced 20 days after deprivation) in that they tried to mount intruder animals. This unexpected finding is paralleled by results obtained in a rat-study (ALBERTS and GALEF, 1971) where ZNSO_4 treated rats were unable to distinguish between familiar and unfamiliar conspecifics and behaved invariably amicably or sexually toward them instead of initiating aggression. These findings raise the possibility that isolating male mice (as well as male rats) predispose them towards amicable and sexual behaviour versus a con-

specific, unless stimuli that release competitive aggressive behaviour, i.e. adult strange male urine, are provided. Another finding, that points towards this end are the results of DIXON and MACKINTOSH (1976) which show that juvenile males' urine does not possess an aggression inhibitory factor, but that these animals are probably passively protected from attacks because their urine does not contain an aggression releasing factor. In this study, ZnSO_4 -treatment differentially affected the various social behavioural elements, depending on whether their expression was associated with physical contact to the opponent. Thus, while elements not involving contact (i.e. focussing of attention toward the other animal or approaching it) were significantly decreased, elements that afford contact (i.e. such as investigating the other animals body) were significantly increased. As a consequence, it is suggested, that the single category formerly used to describe social behaviour (e.g. GRANT and MACKINTOSH, 1963, DIXON and MACKINTOSH, 1971, 1975, DIXON, 1986) may be split into two new categories: "social attention"

(SAT) and "social contact" (SCO). (For the evaluation of cage experiments in this study, the modified ethogram was used already).

2.1.1. Implications for the olfactory sense

While it is known that the olfactory system is a multicomponent one the way it is activated by various olfactants (i.e. the transduction- and recognition mechanism) is still not clear. Basically two different theories can be considered (e.g. ADRIAN, 1953; GLEESON, 1978; MOZELL and HORNUNG, 1984; SHEPHERD, 1985) 1. across-fibre-pattern-theory: This theory assumes a kind of chromatographic analysis of olfactants in the olfactory mucosa where substances would evoke different specific discharge patterns across numerous receptor cell-types (i.e. a system analogous to color vision). 2. labelled-line-theory: According to this theory specialized receptors would be designed to accept only one or a very limited number of specific types of olfactant-molecules and consequently produce a specific excitation (i.e. as encountered in sex pheromone perception in the

silk moth). While the first theory has the obvious advantage of flexibility, i.e. with relatively few receptors a wide spectrum of substances could be encoded, the second system would be more reliable and quick which could be an advantage for the evaluation of substances with signal-value (i.e. releasers) such as pheromones. Our results do not contribute to the resolution of this problem. However, the histological analysis showed that ZnSO_4 -treatment did not affect all subunits of the chemosensory system, but selectively destroyed the primary olfactory mucosa outlining the turbinaria, sparing the secondary mucosa contained in the vomeronasal organ. As already pointed out, however ZnSO_4 -treatment effects become apparent from altered behaviour (i.e. missing aggression) some time before histological changes in the epithelium outlining the nasal cavity can be detected. Nevertheless the conclusion can be drawn, that while this vomeronasal system has been suggested, to play a crucial role in sexual behaviour in the hamster (POWERS and WINANS, 1975; CLANCY et.al., 1984) and in the mediation of puberty-delaying chemo-

signals in female mice (LEPRI et.al., 1985), it has apparently no significant contribution to the release of intermale aggressive behaviour.

2.2. Visually guided behaviour

While visual control of different types of behaviour has been reported for various mammals, such as place navigation by rats (MORRIS, 1984), mice (NEWSOME et.al., 1982) and the golden hamster (ETIENNE, 1985); prey catching in *salamandra salamandra* (LUTHARDT and ROTH, 1983); pattern recognition in rats (THINUS-BLANC, 1978) etc, it was especially the neuroethological approach to the organization of visuomotor behaviour, in non-mammalian anurans (for reviews see e.g. EWERT, 1985; INGLE, 1981a) as well as in small mammals, i.e. rodents (e.g. INGLE, 1981b; SCHNEIDER, 1969) that has been highly productive in analysing the visual control of non-social forms of behaviour i.e. the practical uses of vision by which these animals get around with their everyday world - pursuing prey, negotiating barriers, jumping from rock to rock etc. The two mammals that are most commonly used for neuroetho-

logical studies of visuomotor behaviour are: the gerbil (meriones unguiculatus) and the golden hamster (mesocricetus auratus). The main interest laid on the well structured, foraging- and food recognition behaviour (FINLAY and SENNELAUB, 1981). In the present study it was shown, that in the mouse, vision subserves and is necessary for successful attacking of intruder animals during territorial defense.

Considering the communicative aspect of visual cues in mice, i.e. their signal value in intraspecific social behaviour, little is known and conflicting results (obtained in cages) are reported in the literature: UHRICH (1938) states that blinding dominant mouse-group members did apparently not alter their social status, nor did it interfere with fighting (the same conclusion was drawn from a rat study by BEACH [1942]), while LAGERSPETZ and PORTIN (1968) concluded from their experiments that movement of the target is necessary for aggressive behaviour. Both studies, however, suffer from severe drawbacks. UHRICH's study was coarse, only being interested in the quantitative occurrence of

fighting, without analysing its quality. LAGERSPETZ and PORTIN on the other hand used an unnatural situation for their work, i.e. a bottlebrush as opponent and electric shocks to induce aggression, thus in both cases the naturally occurring stimuli that lead to the type of behaviour observed, were sidestepped. On the other hand, it is well known from ethological analysis, that in aggressive encounters numerous species display body postures which must change their apparent visual size, such as sideways presentations, upright postures etc. Nonetheless, there is so far only one study that seemingly could relate social visual cues to behaviour in rodents. GRANT, MACKINTOSH and LERWILL (1970) suggested, that the size of the black chest patch in hamsters can be linked to success in aggressive encounters. However, an attempt to duplicate these results in the same laboratory failed (cited in: INGLE, 1981b). KALKOWSKI (1968b) tested whether mice are capable of identifying species partners which were accessible only visually, i.e. confined in transparent plexiglass-boxes. Since he could not find "positive social

reactions (whatever the combination of sexes presented) such as approaching more frequently or remaining longer within the field of vision of a particular opponent" he concluded that no individual recognition by visual cues can be achieved by mice. Here he is probably right, but the generalized conclusion that "visual control of the social surroundings in laboratory populations of white mice has no starting point..." cannot be drawn from his experiments, since his mice were not allowed to closely interact. This explains the obvious discrepancy to our findings. Although indeed, vision is of limited use in certain activities associated with agonistic encounters, such as attending, approaching or tracking (probably due to its limited effective distance), it is not only the prerequisite for successful attacking under semi-natural conditions, but it also has a clear modulatory function on aggressive responses in cage encounters. Indeed the results of this study show, that visually deprived cage residents not only show less ambivalent behavioural elements associated with aggression, i.e. "offensive-ambivalence" and "distance-ambiva-

lence" but also the quality of "offense" toward intruders displaying elements of static flight is altered (cf. III.B.3.3.). This suggests that much of ambivalent behaviour of the home-animal is induced by visual cues emerging from the intruder, i.e. the highly conspicuous "upright posture". This finding has an interesting ethological implication. Mice are territorial and in situations where emigration is not possible they frequently live in small demes (ANDERSON, 1964; REIMER and PETRAS, 1967) where usually one despotic dominant reigns over few subordinates. Consequently a mechanism would be expected, by which the subordinates are able to reduce dominants' attacks. Although the ethogram of the mouse comprises no full-submissive posture (which was found to block aggression in rats, GRANT, 1963) a long postulated mechanism in the mouse to reduce the incidence of attacks and bites seems now established in the form of the ambivalence-inducing properties of the upright-postures (UP, DU) as performed by the intruder. It is interesting to note here, that target maps of wounds at the body surface of mice show that

very few bites are delivered to the ventral surface (BRAIN, 1982). In this light, the "cut-off"¹¹ -function attributed to the eye-closure of the dominants during attacks (DIXON, 1986) may be considered acting to reduce the input of ambivalence-inducing visual signals emerging from the intruder. (The alternative explanation that eye-closure simply serves to protect the eyes during attacking cannot be completely excluded, but seems unlikely, since the eyes are normally closed well out of reach of the opponent and are not closed at all by the submissive animal).

2.2.1. Implications for the visual system

The capacity to recognize and discriminate visual patterns is essential for the localization of objects and for appropriate reaction towards changing stimuli such as for example visually salient signals in communication. As long ago as 1907, YERKES found that mice are capable of quite difficult pattern discriminations and BOXBERGER (1953) calculated a mean maximal decision distance from stimuli for these discriminations of about 8 cm. A corresponding value of 4-7

in. was found for pattern distinction tasks in the gerbil (INGLE, 1981b). Our results are in accord with these findings, since it was found that stationary conspecifics could be detected by acoustically deprived mice at distances of about 10 cm, as measured using the grid procedure. However, before attributing general shortsightedness to mice it should be remembered, that the reported measures are all situation specific (i.e. the contrast of white mice in saw-dust is very faint), making it possible, that under other, more natural circumstances, and for other tasks, i.e. navigation by distant cues, different measures might be obtained. Indeed, MACKINTOSH (1973) reports recognition of territorial boundaries of mice by visual cues, presented in the form of black rectangles of a size of 5x7 cm placed at distances of up to roughly 100 cm.

¹¹ The concept of "cut-off" actions (e.g. closing of the eyes) used by an individual to modulate its aggressive and flight tendencies caused by visual stimuli was introduced by CHANCE (1962).

Furthermore the present results show that mice are more susceptible to moving visual cues, since running intruders could be detected by acoustically deprived dominants at distances up to about 18 cm. Since visual behaviour generally seems to be compounded from multiple discrimination and localization processes it would be interesting and rewarding to test whether different characteristics of distinct neural visual systems account for the above finding, in analogy to SCHNEIDER's two visual systems-hypothesis (1969)¹². The analysis of attacking behaviour revealed a predictive visual mechanism in the mouse, i.e. a prediction of the targets trajectory is possible by means of visual cues. A comparative study performed by INGLE (1981) shows that the gerbil also seems to possess an "anticipatory overshoot mechanism". Since tracking in the mouse does not appear to be predictive, a different mechanism must be postulated for predictive attacking, that suppresses the tectum in order to allow its separate mapping system to drive the overshoot. On the basis of the known anatomy in the gerbil the frontal- and the

premotor cortex (areas 24 and 6) were suggested by INGLE to be good candidates for such a system, since each area projects strongly to the stratum profundum (zone for generation of the tectal motor output) in the tectum (INGLE, 1981). While from our experiments no mechanistical explanation can be given, the above suggestion may prompt further investigation of the mouse attacking-system.

12) In 1969 SCHNEIDER could show in hamster-foraging-behaviour, that two behavioural systems can be dissociated by cortical- or tectal-lesions respectively. The initial suggestion of Schneider, that 'localization vs. identification' behaviours of rodents can be dichotomized as 'subcortical vs. neocortical' functions was relativized by INGLE (1981). According to the latter author, 'relative motion detection' is cortically dependent, therefore cortical subsystems must also be postulated to modulate different 'visuospatial abilities' additionally to the SC. Basically however it still seems true, that while the reflexive orienting reaction is in need of a functional retino-tectal system, pattern discrimination relies on an intact retino-geniculate pathway. Schneider's thereupon formulated two visual-systems hypothesis has in the meantime been shown to apply to a greater or lesser degree also to the rat (GOODALE, et.al. 1978), the gerbil (MLINAR and GOODALE, 1984) and to man and may be a universal feature of all higher vertebrates.

Furthermore it now becomes necessary to obtain more information about the main factors, limiting the performance of even peripheral parts of the visual system, since as long as these are unknown, a clarification of (the nature of) the interpretative task that the central nervous system has to perform, remains hypothetical.

2.3. Acoustically guided behaviour

In diurnal animals, the visual system is normally characterised by high spatial resolution power (WALLS, 1963). Therefore in these animals, vision is the most important system in spatial control of social and non-social behaviours. However animals that are active in nearly complete darkness or live in ecological niches, where visual cues are not salient (i.e. as the mouse), have to follow a different strategy. It has become a common finding now, that these species frequently rely on acoustic cues to keep track of distant sources of stimuli, e.g. many aquatic species like fishes (SCHUIJF and HAWKINS, 1976) or amphibians (POPPER and FAY, 1980, pp. 119-205). Others, higher vertebrates, have

developed special mechanisms of considerable sophistication, both for detection and localization of objects and conspecifics. Examples are: sonar hunting in bats or sonar detection of objects in bats (for a review see e.g. GRIFFIN, 1958) and blind dolphins (e.g. BUSNEL and FISH, 1980), and hunting by passive listening in the barn owl (e.g. PAYNE 1971). The mouse can now be added to this list. The present results clearly show, that in the mouse the acoustic system is not only sufficient to serve the localization and tracking of distant cues generated by conspecifics, but is necessary for this task. Although the accuracy of acoustic tracking (PAT) may have been slightly overestimated by exploiting smoothed data and although the resolution of video analysis in the time domain is somewhat coarse ($\Delta t=40\text{ms}$), PAT certainly comes up to the task of accurately tracking an intruder until an attack can be delivered.

Whilst the bat uses an active tracking system to hunt insects (i.e. by emitting itself an acoustic signal and evaluating the reflections), the owl relies on a different strategy during predation. Here the system was

found by PAYNE and DRURY (1958) to be a passive one (i.e. the acoustic signals evaluated by the owl, stem from the rustling movements of the prey). Thus, the owl acoustic hunting system seems to be in remarkable analogy to the now revealed acoustic tracking system in the mouse, although the task is much more difficult for the owl, since it has to localize in 3-dimensional space, while the mouse only has to localize in 2-dimensional space.

2.3.1. Implications for the acoustic system

A good deal of auditory research has already been done on mice from many perspectives. Thus such topics as peripheral- and central anatomy, -physiology, psychoacoustics and sound communication have received wide attention and the reader is referred to the basic book: "The auditory psychobiology of the mouse" by J.F. WILLOT (1983), for a detailed review of current knowledge. The general sensitivity of the acoustic system, which is of interest in view of acoustic tracking, has been investigated using several behavioural techniques, i.e. pryer reflex, heart

rate conditioning, suppression of water licking, etc. as well as electrophysiological investigations of cochlear nucleus (CN) and inferior colliculus (IC) etc. (summarized by EHRET, 1983). These studies of sound perception in laboratory mice revealed two sensitivity peaks of the acoustic system, one at 15kHz and a second one at about 50kHz (MARKL and EHRET, 1973), the sensitivity at 15kHz reaching almost 0dB (SPL)¹³. Although it is realized that acoustic sensitivity may vary between different laboratory strains (EHRET, 1983) and it is not sure, whether the obtained results on the sensitivity of the acoustic system also holds for biologically significant stimuli, this result could explain our finding that visually deprived animals can use very faint noises made by conspecifics to localize and track them.

13) Sound pressure is measured in Pascal (Pa = N/m²). The standard adopted internationally is 20 Pa, roughly the threshold of human hearing for a 3 kHz tone. Acoustic signal levels are conveniently expressed relative to this standard as dB (SPL), i.e. $= \ln ?\text{Pa}/20\text{Pa}$.

The cues that an animal can use in acoustic localization will depend upon the frequency range of its hearing, the size of its head, configuration and mobility of external ears, as well as upon the acoustic spectrum of the sound source (see e.g. Knudsen, 1980). From our experiments it cannot be concluded whether PAT can use single tones or whether it is only functioning on broad band noises. Masking experiments or others that use single frequency tones as stimuli would be needed for such an answer. EHRET and DREYER (1984) found that mice are well capable of localizing and approaching a loudspeaker by pure tone stimuli, and single tone localization was also found in the owl (KNUDSEN, 1980). However, the accuracy shown by the mouse in these localization tasks was greatest, when broad band white noise stimuli were presented. Thus the conspecific noise in sawdust can be assumed to provide an ideal source for sound localization due to being extremely wide-band, i.e. reaching from about 50 Hz to 100 kHz (cf. Fig. 14 section III.3.2.1). Additionally, open loop approach to the loudspeaker was found to be

impossible in the above reported study. Although this finding again parallels our results, it has to be added that, (as will be discussed in sect IV.5.), sound localization or -approach tasks may rely on sensory- motor-interfacing systems, basically different from the one used for tracking. This may also explain the result obtained in the owl, showing that these animals are capable of open-loop tone localization (KNUDSEN, 1980), successful predation not being possible when the prey stopped moving before the owl had taken off from the perch. Target tracking by the big brown bat (*epptesicus fuscus*) was found to be a closed loop mechanism (MASTERS et.al., 1985), the features paralleling the findings of this thesis. Section 3.2.1.1 of the results raised the question, as to how a territorial mouse achieves sufficient accuracy in monaural tracking of sounds located ipsilateral to the intact ear? The results suggest, that a successive strategy (i.e. scanning of the sound source) can be dismissed. A relatively simple but rather crude way would be to transpose the loudness of the perceived sound (which would directly depend on the direc-

tional sensitivity of one ear) into a turning response. However unilaterally perceived loudness not only depends on the spatial direction of the sound but also on the distance to the source and on the position of the mobile pinnae. Thus, the tracking mouse should tend to hold the latter two parameters constant. And indeed, in section III.3.2.1 it was found, that the tracker seems to hold a constant distance to the intruder (42 ± 11 cm) and furthermore, this distance is depending on the substrate, the mice are running on. Thus, in trackings performed

on the bare concrete floor, this tracking-distance was found to be 32 ± 9 cm, suggesting that the mouse uses an internal set point for an optimal loudness of the source to be tracked. The pictures presented in Fig. 39 show, that in addition the tracker holds its ears in a fixed, laid-back position during tracking (Fig. 39b), while during "attending" the ears assume a forward direction (Fig. 39a). Related to the above hypothesis may be the finding of STIEBLER and EHRET (1985) that in the inferior colliculus (an important midbrain acoustic

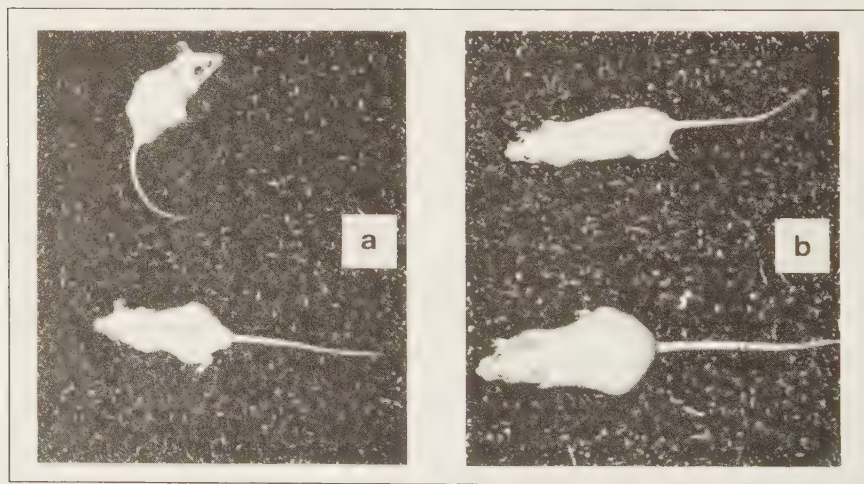


Fig. 39 Photographs taken from mice in enclosures during attending and approaching (a) and during tracking (b), demonstrating the difference in ear-position during these distinct behavioural actions. Commentary see text.

relay station) parallel, horizontal iso-intensity planes can be found, each covering a wide band of frequencies. These planes could then directly be read out to generate corresponding turning-signals for tracking behaviour.

There remains another interesting question related to acoustic tracking, which at present we cannot answer: How does the tracking mouse dissociate self generated noises from the ones emerging from the intruder? Both noises cover the same frequency-spectrum, unlike in prey hunting of owls (which have also been found by Payne and Drury [1958] to use a passive acoustic hunting system), where wing-beat frequency of the predator is clearly distinct from the frequency range of rustling noises made by prey-mice. Three possible solutions to this enigma are conceivable: 1. the body, and in part the ears in their backward laid position, shield some of the self-generated noise, allowing the intruder-associated noises to reach the ear drum with a higher intensity, or 2. an active neural mechanism suppresses the detection of self-generated signals. (Such a sophisticated mechanism was e.g. found in electric fishes,

where a corollary discharge of electric signal emission is used to cut off the detection system during emission phases [HEILIGENBERG, 1984]), or 3. extracting information from a combination of white noise generated by both, the escaping animal and the tracker itself. This superposition of noises might result in a change in the relative frequency content of the correspondingly perceived noise, as was shown by WILSON (1966). Such a system could then be achieved without having a sophisticated separation of self-generated and target noise.

2.4. Tactile control of agonistic behaviour

Vision is, however, not the only sensory modality used to direct or modulate aggressive behaviour during close interaction with the opponent. From section III.B.3.4. we know, that cutting the whiskers had an effect opposite to the one found for visual deprivation. Thus "vib-dep"-animals showed significantly increased ambivalent behaviour and more "threats", while the number of bites was reduced (cf. appendix A). Furthermore a clear relationship between eye

closure and vibrissal contact was observed during performance of the behavioural elements "offensive sideways posture" and "bite" (cf. section III.B.3) indicating that the ultimate positioning of bites is under vibrissal control and an intense interplay of vision and

Our results are in accord with findings of THOR and GHISELLI (1975) of reduced shock-induced fighting in devibrassated rats but oppose to those of BRAIN et. al. (1982) performed on white laboratory mice. However the latter results, showing



Fig. 40 Photograph, showing the sensory interplay between the visual and tactile sense during the "offensive sideways posture" in the animal on the right hand side. Note, that the eye on the side having vibrissal contact is closed, while the other eye remains open. (Photograph by courtesy of Miss C. Huber).

somatic sense during attacking takes place in cages. Fig. 40 shows the aggressive animal (on the right hand side) with the eye closed on the side where vibrissal contact with the intruder-animal is established during an "offensive sideways-posture".

that naive (in regard to fighting) devibrassated males, rendered aggressive by isolation, showed a tendency toward decrease attacking behaviour, whereas fighters trained during the isolation period tended to show a higher incidence of attacking, are

somewhat ambiguous. First, the analysis did not separate "biting attack" into sub-elements, as we did. Indeed, had we not separated "offensive ambivalence" from "offense" no significant difference between controls' and deprived cage residents' behaviour could have been detected since manipulation of vibrissal input raised ambivalent behaviour, while it is suppressed straightforward "offense". Second, the assumption of naive animals in their work has to be regarded with care, since these animals were kept in group cages up to an age of 43 days and may almost certainly have gathered some fighting experience before isolation took place.

2.4.1. Implications for the tactile sense

Since their description by WOOLSEY and VAN DER LOOS (1970), a variety of anatomical, electrophysiological and developmental investigations have combined to show that there is a one-to-one correspondence between a rodent's individual vibrissae and barrel-shaped cell clusters in its contralateral primary somatosensory cortex. Thus spatial sensitivity should be in-

herent in the system. The results of this study, obtained from experiments, aimed at removal of peripheral vibrissal input, seem to testify this. The vibrissae seem to provide a clear spatial representation of conspecific intruders to the aggressive cage resident animal, since bites can be delivered using tactile feedback from the intruder provided by the vibrissae and significantly less bites are delivered by aggressive animals whose vibrissae had been removed.

3. Sensorimotor-interfacing and tracking

In recent studies centered on the superior colliculus (SC), this structure was found to carry a representation of spatial sensory maps of various modalities, i.e. acoustic-, visual- and tactile sense and in pit vipers (*crotalinae*) even of the infrared sense, in register with each other. Furthermore, the deep layers of the SC are connected with a multitude of structures that are related to visual, auditory and somatosensory function and to motor maps of eye- and in some species head- and pinna-movements (PALMER and KING, 1982: for the guinea pig; DRAEGER and

HUBEL, 1975; for the mouse; MEREDITH and STEIN, (1983): for the hamster; HARRIS, BLAKEMORE and DONAGHY, 1980, HUERTA and HARTING, 1984: for the cat and JAY and SPARKS, 1984: for the monkey). Thus a simple superimposition of such sensory- with motor maps could be a simple yet elegant mechanism for the generation of certain reflex-like types of behaviour. This could in fact be demonstrated in lesion- or electrophysiological stimulation- studies where deep regions of the SC were found to code for reflexive movements of body parts, resembling orientation or escape (SAHIBZADA, 1986). Ever since, the SC has become a point of major interest in neuroethological studies, i.e. especially of rodent visuomotor behaviour. MEREDITH and STEIN (1983) report response enhancement in certain deep-laminae SC-cells by concurrent stimulation of the acoustic and visual system in the same spatial region, thus it seems likely that by pooling a variety of sensory inputs, one population of SC cells may amplify these effects of subtle environmental changes to ensure an appropriate response, even when individual

cues are near threshold. With respect to above considerations it may be important to notice, that binaurally exploited spatial zone was found in the present study to be 40°, centered by the head axis and thus corresponds to the binocular zone of the same size as found by DRAEGER (1978).

The above statements, the knowledge of spatial tuning of auditory neurons in the superior colliculus of the bat (WONG, 1984) and further knowledge that unilateral lesions in the SC caused sensory neglect in the contralateral hemifield (probably due to abolished output of the deep SC motor structures) seem to suggest that the SC is not only the integrating sensory relay station to motor output for reflexive turning of body-parts, but plays a central role in the modal action patterns of acoustic tracking (i.e. PAT, and thus involving whole body motor patterns) an interesting one. Although in our experiments we did not attempt to differentiate between structures lying at various depth in the SC but rather tended to lesion the whole colliculus, indeed, our results from dominant territory holders lesioned unilaterally or bilateral-

ly in the SC, or in various control brain-regions (including the MGB), support this idea. That the observed inability of tracking might be attributable to unintended lesions of brain-structures adjacent to the SC seems unlikely for the following reasons: Since acoustic localization of a conspecific and subsequent approach was not impaired, indicating that neither structures relaying acoustic information to the cortex, nor motor structures necessary for the behavioural expression of cortical acoustic processing were affected. Furthermore, neither Pryer-reflex (both pinnae) nor acoustic startle response were found to be impaired by the lesions inflicted, indicating that brainstem structures processing acoustic and motor information were left intact.

One problem may, however, arise from the above hypothesis relating the registered maps of visual and acoustic space and subsequent motor output in the SC to tracking. As POEPEL (1973) pointed out, visual and auditory space should be "torn apart", every time the animal moves its eyes and thus the median plane of the visual system

is brought into a different direction from the one of the head-axis-centered acoustic system. There are different conceivable ways to solve this problem. In the cat it was found, that each saccadic eye movement starts near or to the center of the orbit and thus a complicated coordination and compensation of the visual and acoustic spatial representations is not necessary (HARRIS et.al., 1980). In contrast in monkeys (macacca mulatta) auditory receptive fields were found to change with eye-position (JAY and SPARKS, 1984). For the mouse, it is not known, whether eye movements occur at all, although rectus muscles are clearly present (WALLS, 1963). Since mice however are assumed to have afoveate eyes (although a visual streak is present) there is probably no need for eye movements during shift of visual attention (i.e. during tracking) since the whole head may be turned and thus making a compensatory mechanism obsolete.

4. Two acoustic-systems-hypothesis

Our lesions placed either in the medial geniculate nucleus (MGN: an acoustic relay station in the thalamus) or in the superior colliculus, allow a further conclusion. In analogy to the visual system, where the two major systems: the geniculostriate- and the retino-tectal system parallel each other (SCHNEIDER, 1969) serving different sensoriphysiological and behavioural functions, suggest that parallel acoustic systems can also be found, i.e. the colliculo(IC)-colliculo(SC) system (i.e. tectal system) and the colliculo(IC)geniculate-cortical system (i.e. cortical system). While the former system (partially unmasked in our experiments by unilateral MGN-lesion) i.e. the acoustic tectal system seems suited to organize reflexive shift of attention towards a sound source, and thus be a necessary prerequisite for tracking, the cortical system (unmasked by uni- or bilateral tectal lesions) is suitable to detect and approach intruders. The internal shift from one system to the other becomes clearly apparent during territorial defense by unilaterally SC-lesioned

dominants. As long as they perform acts of non social behaviour their actions seem completely normal. Also their detection of and approach towards intruders seems normal, but as soon as the intruder flees and thus the territory holder should start tracking, circling ensues (cf. Fig. 24, section III.A.). Thus, a two acoustic systems hypothesis can be added to the two-visual systems hypothesis.

Since KEVERNE (1978) also suggested dual systems for olfaction and taste, we can extend this idea further by proposing, that it may be a general feature of mammals that the sensory-motor-interfacing systems are present in parallel channels. One system of each modality being of a subcortical nature and representing a remainder of a former stage of phylogeny and the other system, a more recent improvement of it, being concurrent with cortical development and serving new and more sophisticated tasks. Rodents are at an intermediate phylogenetic level between animals whose behaviour seems to be more of a type reflexively answering external stimuli (e.g. toads) and primates with cognitive filtering capacities

and further abilities to plan actions in time and space. Thus, an analysis of some of rodents' neural networks may allow a statement representative for mammals in general. Therefore these animals seem to be an ideal tool for mapping behavioural changes and certain actions onto structural identity.

5. Methodological issues

5.1. Olfactory deprivation (ZnSO₄-Solution)

Since there has always been major interest in mammalian olfactory-controlled behaviour, a rich variety of surgical, non-surgical, chronic and reversible techniques suited to abolish the sense of olfaction have been developed over the years, i.e. nerve section, olfactory bulb ablation, destruction of the olfactory epithelium. Due to the multicomponent nature of the chemosensory system the effects produced by the various techniques can be suspected to vary widely and indeed, corresponding effects on social- and non-social behavioural performance are of great diversity. Nowadays, probably the most frequently applied techniques are those of bilateral olfactory bulbectomy

and the coagulation of olfactory mucosa, preferably with 1-5% ZnSO₄-solution. The first method, regarded as being complete and permanent in disrupting olfactorily mediated behaviours, clearly provides a severe intervention and is reported to have many additional effects. Thus non-social behaviour and experimental performance of bilateral bulbectomized animals in learning tasks can change dramatically (MARKS et.al. 1971). The sensitivity to many external stimuli increases, i.e. rats are reported to become hyperemotional and irritable (e.g. BEACH, 1942). These findings could either be due to "psychological stress" associated with total loss of important environmental feedback-information (DOUGLAS et.al. 1969) or to the commonly found alterations in unoperated brain areas, such as widespread changed neurotransmitter levels (CAIRNCROSS, et.al., 1975; HIRSCH, 1980). Thus bulbectomy produces many more effects than a simple sensory deficit and is probably not an ideal technique for experiments of the type reported here.

The ZnSO₄-technique, on the other hand, was long thought to

introduce less grave, only peripheral and reversible effects (SMITH, 1938, CAIN, 1974). Furthermore it was suggested to spare the vomeronasal organ mucosa (testified by our results), thus making the technique suitable for olfactory-deprivation experiments¹⁴. Nevertheless some controversy concerning long-term and central effects of this technique still exists. MATULIONIS (1975) monitored regeneration of the olfactory mucosa after ZnSO_4 deprivation in terms of thickness of the mucosa, which he found to be normal after about 28 to 42 days, depending on the mouse-strain, used for experimentation. His 1976 light- and electron-microscopic analysis revealed most advanced neuronal degeneration 24 to 72 hours after deprivation. The first signs of regeneration in the form of simple squamous epithelial cells containing mitotic figures with a partially low stratified epithelium 48 to 72 hours after deprivation. Thus ongoing degenerative processes seem to occur in parallel with the first signs of regeneration. Quite differently, HARDING et.al. (1978) reported long lasting histological, neuronal and beha-

vioural effects of ZnSO_4 -treatment. Three weeks after deprivation, a complete disruption of the normal epithelial structure was noted, with occasionally occurring small islets of thickened atypical epithelia approximately 40-60 μm thick (normal ca. 100 μm). Furthermore a significant weight loss of the olfactory bulbs was found alongside reduced levels of carnosine synthesis and transport into the olfactory pathway. Some of these alterations were still present 1 year after deprivation (i.e. olfactory bulb shrinkage).

14) In recent years an alternative method to the use of ZnSO_4 for the destruction of the olfactory mucosa, apparently producing the same effects was introduced by the working group of B. REHN, W. BREIPOHL, U. SCHMIDT, Ch. SCHMIDT and F. EFFENBERGER, using the highly volatile N-methyl formimino methylester (MFM). While light-microscopic and electron-microscopic histological studies of the treated mucosa as well as measurements of the olfactory threshold after MFM application have been performed, no behavioural experiments are yet available. However the narrow range between effective and lethal dose of MFM and its high volatility that demands special care during application (since it also affects human olfactory mucosa), so far seem to have prevented widespread use.

Behavioural performance in a food-pellet localization task had by then returned to normal. The discrepancy of these findings compared with those of MATULIONIS, is probably explained by the different ZnSO_4 concentration used in the two studies (1% in the former and 5% in the latter study) and by the different ZnSO_4 -application technique. The latter results correlate with our own, suggesting that although the effects of ZnSO_4 seem less grave than those of bulbectomy, consequences going beyond simple peripheral anosmia can not be denied. Our results suggest that histological signs of regeneration can be seen from day 20 on, and although being quite rudimentary and not yet involving formation of specialized epithelial cells, already allowing release of aggressive behaviour. SIECK and BAUMBACH (1974) warned of possible intoxication of treated animals by ZnSO_4 swallowed during deprivation. However, this can apparently be avoided by our special application technique, where excess ZnSO_4 -solution is permanently sucked off through the mouth, and is unlikely to be the cause for the results obtained in

this study, since treated animals seemed not generally depressed in their behaviour.

5.2. Visual deprivation (contact lenses)

Although the design of contact lenses for small mammals has been reported before (BONNET, 1973) - though of a different kind - their use in animal experiments of the type reported here has been rare. The common methods of introducing visual deprivation have been nerve section, enucleation and lid-suture. These techniques not only involve crucial insult to the animals but also are generally permanent and cause widespread retrograde degenerative processes, unlike the contact lens technique, which is not only quick, reliable, cheap and entirely reproducible but allows one to reinstate visually guided behaviour after removing the lenses (STRASSER and DIXON, 1986).

When the deprived animals awake from short Halothan-narcosis, induced to fit the lenses, they sometimes draw their forepaws over their eyes, but as the eyes are closed no lense-displacements or injury to the cornea can be found, and after

about 5 min. the lenses are generally well tolerated. In normal experiments, the lenses remained in place for about 1 hour and no adverse effects could be observed upon removal. In some experiments mice wore the lenses for 3 weeks. 40% of these animals showed some corneal dullness to varying degrees, but this disappeared 1-2 days later and the animals apparently regained normal sensory capacity. These findings attest to the good tolerance of the method (section II.3.3.) and make it an interesting and "least discomforting" alternative to the more harmful methods mentioned previously for visual deprivation.

Although control animals were not equipped with transparent contact lenses (clear cellulose acetate foil would still alter the refractive index of the peripheral optic apparatus and thus could not serve as control) this does not invalidate our results, since animals wearing opaque contact lenses only showed reaction specific behavioural defects.

5.3. Acoustic deprivation (ear-plugs)

Besides acoustic nerve ligation the use of ear-plugs has been a common procedure to introduce acoustic deprivation (e.g. SHNERSON and PUJOL, 1983). Although it is known, that ear plugging does not completely abolish acoustic noise detection, but apparently introduces a sound-attenuation of between 25 and 35 db this seemed to be sufficient for our work, since after deprivation no behavioural response to conspecific acoustic signals or noises seemed to be present (cf. A+V-dep in section III.A.2.3.).

Since all silicone rubbers contain acetic acid, this could be expected to irritate the outer ear canal of the deprived animals and induce some discomfort. However our deprived animals showed no signs of excessive grooming or other signs indicating discomfort (as long as the pinna was not crusted with silicone rubber, which obviously disturbed these mice), but quickly resumed search for intruders upon reintroduction into their territory. In some animals the ear-plugs remained in place for 2-3 days. These animals

frequently tried to get rid of the plugs, but this was probably rather due to acoustic deprivation rendering them susceptible to the attacks of conspecifics, than due to skin irritation. Examination of outer ear meatus after removal of the plugs revealed no macroscopic alterations in animals carrying ear-plugs for up to 3 days.

As in visual deprivation, behaviour altered by plugging the ears was highly reaction specific (i.e. attending and tracking were affected) leaving other behavioural elements such as attacking, unaffected. Thus plugging does not seem to exert unspecific effects that could disturb the results. Consequently, ear plugging as described here, provides an easy, and fully reversible method, suitable for the deprivation of the acoustic sense.

V. EPILOGUE

Although the present study shows, that behavioural observations of the type reported here, that provided the guidelines for subsequent neurophysiological and neuroanatomical studies, leads to the recognition of the mouse being another example of an animal whose analysis of behaviour in a neuroethological approach seems rewarding. However some questions associated with our findings yet remain unanswered and many new ones appeared during the course of the current investigations.

For example the spectral characteristics of the stimuli suited to provide PAT with the necessary input is not yet clear, i.e. tonal- vs. broadband-noise stimuli, the effective spectral band etc.

The neural correlate for attacking behaviour has not yet been investigated. However, a pilot study performed on 2 mice receiving wide destruction of striate cortex (while SC lesion was intended but not achieved) showed, that successful attacking

behaviour was absent in these (not sensory deprived) mice, suggesting that attacking may be attributed to a cortical mechanism. Rodent visuomotor behaviour has proved to be a powerful tool in analysing parallel sensory subsystems. Nevertheless knowledge on stimulus processing and interactions of these systems has not yet surpassed the hypothetical stage. Thus it remains to be investigated in further electrophysiological- or lesion-experiments, how tectal and cortical systems interact during tracking and attacking of a conspecific in the mouse.

During the enclosure experiments it was astonishing with what certainty the visually deprived mice dodged and detoured objects during tracking, often taking routes different from the ones of the fleeing intruders (this was also the case when new objects were introduced into the territory). Thus it would be interesting to know whether a system similar to PAT would also be suited for barrier detection by perception of running noise, reflected from objects (i.e. an echolocation system). Preliminary investigations (not presented) seem to attest just that, since SC le-

sioned mice frequently bumped into walls and objects.

Thus, coming back to SNELL (1941), cited in the introduction, it seems well probable, that the common mouse still holds the key to many more issues related to sensory processing and sensory-motor interfacing in mammals.

VI. SUMMARY

1. Intermale mouse agonistic behaviour was investigated under semi-natural conditions (i.e. territorial defense in enclosures) as well as in cages. Behavioural interactions were video-recorded and analysed in terms of the acts and postures shown by the animals.

2. It was found that (depending on space available) mouse aggressive behaviour can be expressed either in a dynamic type of aggression (as seen in enclosures) or in a static type of aggression (as observed in cages in this study). Dynamic aggression could further be structured into distinct subunits (i.e. behavioural phases): 1. detection/localization-phase, 2. approaching-phase, 3. tracking-phase, 4. attacking-phase (Figs. 8 and 37).

3. To examine the sensory physiological correlates of various behavioural elements or -phases, deprivation experiments were performed, using opaque contact lenses to exclude vision, silicone rubber ear-plugs to exclude audition and flushing the

nasal mucosa with a 5% ZnSO_4 -solution to abolish olfaction.

4. From cage experiments it became clear, that olfaction was crucial for mice to show any sign of aggressive behaviour at all (Fig. 29). Selective deprivation of the various senses exerted profound impairment of the above phases (point 2) as seen in enclosures, albeit to differing degrees, suggesting that generally a specific sensory modality predominated and thus indicating that the above phases are not merely arbitrary, but represent physiologically distinct although functionally related events. Thus, detection/localization as well as approaching and tracking (chasing) were found to depend primarily on audition, whereas for attacking functional vision was necessary (Figs. 9 and 10).

5. Frame-to-frame analysis of tracking behaviour in visually deprived animals showed, that mice seem to possess an efficient acoustic tracking system (named passive acoustic tracking PAT), similar to the one used by the owl (*tyto alba*) to track its prey (Fig. 12). The system is effective within a distance range up to ca. 100 cm (depending on the substrate

the animals are running on) and works on a closed loop basis. During tracking, the angular position in acoustic space of the target (intruder animal) is continuously translated into the angular velocity of the tracking mouse, with a latency of about 100ms (Figs. 15 and 16).

6. The tracker holds a roughly constant distance of 42 ± 11 cm to the leader (on saw-dust) and when the former's body is in line with the latter's and at a distance of 30-40 cm, the territorial mouse accelerates, to bring the fleeing intruder within the range of the visual system, to launch the attack.

7. Monaural tracking is partly possible, suggesting (with the exception of a central sector of about 40° where binaural signal processing is performed) a simple mechanism of spatial localization during acoustic tracking, i.e. perceived loudness in one ear, may be translated into spatial location on the ipsilateral side (Figs. 18 and 19).

8. Visual tracking (Fig. 20) is possible, but is of limited use, since it only works within distances of up to 20 cm between the leader and the tracker.

9. In contrast to tracking, attacking may be predictive, i.e. the territory defending mouse can predict the intruder's trajectory and calculate the collision course (Fig. 22) Attacking under close-encounter condition (i.e. in cages) reveals cooperation of visual and tactile cues (table 6).

10. In search for a neural correlate of acoustic tracking, lesion experiments were performed. These revealed that an intact superior colliculus is necessary for acoustic tracking, while it is not for approaching (Figs. 24 and 25).

11. Since however acoustic tracking seems not hampered by lesions placed in the medial geniculate nucleus, parallel acoustic pathways are suggested, subserving different behavioural actions and a parallel may be drawn to the long known two visual systems hypothesis.

VII. APPENDIX

1. Appendix A

Raw data, expressing frequencies and durations of all elements contained in table 4. Arrangement of data and statistics according to the example below.

P O S - A N A L Y S I S

EXPERIMENT : G=CA

COMPOUND : 100.503

DATE : 27.06.85

OBSERVER :

NUMBER OF TREATMENTS : 2

TREATMENT 1 (TR1) : control

NUMBER OF ENCOUNTERS : 15

TREATMENT 2 (TR2) : vis-dep

NUMBER OF ENCOUNTERS : 15

REMARKS :

STATISTICS :

e.g. 15.4+ 3.2

12.0 # H*= 11.9 ###

15.4 : MEAN 12.0 : U-VALUE

3.2 : SEM 11.9 : H-VALUE corrected

U-TEST : ## 0.01 >= p

0.05 >= p > 0.01

p > 0.05

H-TEST : ### 0.01 > p

0.025 > p >= 0.01

0.05 > p >= 0.02

0.1 > p >= 0.05

> p >= 0.1

ETHOGRAM : POTA02

SAT SOCIAL ATTENTION

OFF OFFENSE

DIA DEFENSIVE AMBIVALENCE

	TR1	TR2
AT	40.4+3.1	17.1+2.3
SA	5.3+ .3	10.0+ .5
AP	27.6+4.4	2.1+ .7
TU	2.7+ .5	4.0+ .5
TOT	71.4+ 6.0	32.4+ 2.9

SDC

DURATION

SDC NON-SOCIAL

	TR1	TR2
SC	9.5+ .5	2.5+1.3
SR	1.6+ .1	2.2+ .1
SH	0+ .0	80.0+ .2
SP	2+ .1	5.5+ .5
SA	0.0+0.0	62.5+ .6
DK	1+ .1	1.1+ .8
SI	2+ .2	7.3+7.2
SU	2.6+1.7	37.5+1.3
SAP	3+ .1	4.4+1.0
PD	0.0+0.0	60.0+2.7
RO	2+ .1	1.0+ .6
SC	51.0+10.0	39.9+ .4
DI	3+ .2	7.5+3.0
EX	47.6+4.9	111.6+7.7
LV	5+ .2	100.5+ .2
VA	14.7+2.6	17.8+2.9
FP	1+ .1	100.0+0.0
DP	0.0+0.0	0.0+0.0
LS	3+ .2	112.5+ .0
AJ	0.0+0.0	0.0+0.0
AL	0.0+0.0	0.0+0.0
AS	0.0+0.0	112.5+ .0
TOT	119.2+11.8	255.5+10.3

SDC SOCIAL CONTACT

	TR1	TR2
IM	10.4+3.4	19.3+2.6
MO	5.4+1.8	16.3+1.0
GR	1+ .1	99.8+ .3
SH	4.4+2.6	2.4+ .6
TOT	20.3+6.3	36.9+3.6

SEX SEX-RELATED BEH

	TR1	TR2
FO	8+ .4	4.7+1.0
AM	1+ .1	40.5+ .5
MT	0.0+0.0	0.0+0.0
GC	0.0+0.0	0.0+0.0
PL	2+ .2	112.5+ .1
CO	0.0+0.0	0.0+0.0
PF	1+ .1	112.5+ .1
TOT	12+ .6	50+1.0

	TR1	TR2
TH	4.3+1.0	7.2+ .1
AK	2.7+ .5	15.0+ .5
BT	23.2+3.7	2.4+1.5
CH	1.7+ .6	10.0+ .5
AG	1+ .1	104.0+ .1
TOT	32.1+3.9	50+1.9

OFA OFFENSIVE AMBIVALENCE

	TR1	TR2
OS	21.5+3.3	1.2+ .7
OU	2.7+ .6	13.9+ .1
PY	7.8+1.6	1.0+ .6
SP	2.3+2.3	1+ .1
TOT	34.1+4.9	2.4+1.0

DIA DISTANCE AMBIVALENCE

	TR1	TR2
ZZ	6.9+ .8	1.4+ .1
GI	5.2+1.3	0.0+0.0
VR	8.9+1.9	1.1+ .6
EA	5.8+1.0	2.0+ .5
TOT	26.8+2.6	1.3+ .7

	TR1	TR2
OA	6+ .2	3+ .1
UP	2+ .1	101.5+ .4
DU	0.0+0.0	0.0+0.0
DS	0.0+0.0	1+ .1
TOT	8+ .2	11+ .5

ARF ARRESTED FLIGHT

	TR1	TR2
CR	0.0+0.0	1.4+ .6
FR	32.8+8.3	15.9+2.9
KE	0.0+0.0	1+ .1
SL	0.0+0.0	112.5+ .0
TOT	32.8+8.3	17.4+2.9

ESC ESCAPE

	TR1	TR2
EG	2+ .1	7.2+ .1
EV	8+ .4	2.6+1.0
RT	11.8+1.7	65.0+ .6
FL	0.0+0.0	0.0+0.0
OW	1.0+ .6	85.0+ .2
TOT	13.8+1.0	13.6+2.0

EXPERIMENT - GAMCA			SVT SOCIAL ATTENTION			OFF OFFENSE			DEA DEFENSIVE AMBIVALENCE		
NUMBER OF TREATMENTS - 2			TR1 TR2			TR1 TR2			TR1 TR2		
TREATMENT 1 (TR1) : CONTROL			AT 26.1+ .8 14.3+ 1.7			T0 4.9+ .7 11.0+ .6			08 4+ .2 89.3+ 1		
NUMBER OF ENCOUNTERS : 15			SA 5+ .2 87.5			AK 4.7+ 1.3 20.5+ .3			UP .7+ .3 89.5+ 2		
TREATMENT 2 (TR2) : SELF-DEF 44d			AF 15.7+ 2.1 5.0+ 1.1			BT 23.8+ 2.1 3.5+ .3			DU 0.0+ 0.0 91.3+ 1		
NUMBER OF ENCOUNTERS : 15			TU 3.9+ .7 28.0+ .5			CH 3.9+ .6 0.0+ 0.0			DS 1+ .1 97.5+ 3		
WORK FREQUENCY			TR1 TR2			TR1 TR2			TR1 TR2		
NSD NON-SOCIAL			TOT 46.3+ 2.2 22.9+ 2.7			AG 2+ .1 95.5			DS 104.5		
			10.0+ .0			10+ 1.0			TOT 11+ .4 9+ .6		
			10+ 18.2+ .000			TOT 37.5+ 3.0 3.3+ 2.1			10+ 2+ .0		
			3.0+ .0			10+ 21.2+ .000					
SGO SOCIAL CONTACT			TR1 TR2			TR1 TR2			TR1 TR2		
			IN 5.5+ 1.4 13.5+ 2.3			OS 29.1+ 2.8 1.1+ 2.9			CR 0.0+ 0.0 90+ .2		
			MO 4.5+ 1.0 13.1+ 1.5			OU 5.9+ .9 4+ .3			PW 16.5+ 2.1 4.5+ 1.1		
			CA 0.0+ 0.0 5.5+ 1.1			PY 8.8+ 1.4 26.0+ .5			RE 0.0+ 0.0 1+ .1		
			SM 2.4+ 1.0 4.6+ 1.3			SP 1+ .1 96.0			SL 0.0+ 0.0 0.0+ 0.0		
			TOT 12.4+ 2.7 36.5+ 3.2			TOT 63.9+ 4.4 5.9+ 4.6			TOT 16.5+ 2.1 4.9+ 1.3		
			28.5+ .0			14.0+ .0			27.5+ .0		
			10+ 12.2+ .000			10+ 16.9+ .000			10+ 12.5+ .000		
SEX SEX-RELATED BDN			TR1 TR2			TR1 TR2			TR1 TR2		
			FO 1.7+ .4 5.4+ 1.5			Z2 7.5+ 1.5 3+ .3			PC .5+ .2 1.6+ .4		
			AM 0.0+ 0.0 40.0+ .9			CI 6.6+ 1.2 5+ .5			EV 0.0+ 0.0 41.0+ .8		
			MT 0.0+ 0.0 8+ .6			WR 5.9+ 1.2 1.3+ 1.0			RT 16.8+ 1.6 7.8+ 1.1		
			OG 0.0+ 0.0 97+ .5			BA 8.7+ 1.9 1.1+ 1.1			FL 0.0+ 0.0 105.1+ .1		
			PU 0.0+ 0.0 6+ .2			TOT 28.7+ 3.4 12.5+ .0			OW 1.5+ .5 3.0+ 1.7		
			GO 0.0+ 0.0 97+ .5			14.0+ .0			85.5		
			PP .3+ .2 8+ .3			10+ 5.8+ .000			TOT 18.8+ 1.5 16.9+ 1.6		
			80.0			10+ 2.1			72.5		
			TOT 2.0+ .4 9.5+ 2.7			54.5+ .0			10+ 2+ .0		
			54.5+ .0			10+ 5.9+ .000					
NSD NON-SOCIAL			TR1 TR2			TR1 TR2			TR1 TR2		
			SG .9+ .3 1.5+ .6			WA 6.7+ .6 11.1+ .9			PC .5+ .2 1.6+ .4		
			SR .1+ .1 109.5			PP 0.0+ 0.0 112.5			EV 0.0+ 0.0 41.0+ .8		
			SH 0.0+ 0.0 2+ .1			DP 0.0+ 0.0 0.0+ 0.0			RT 16.8+ 1.6 7.8+ 1.1		
			JP .2+ .1 90.0			LS .1+ .1 103.0			FL 0.0+ 0.0 105.1+ .1		
			EA 0.0+ 0.0 6+ .3			A3 0.0+ 0.0 0.0+ 0.0			OW 1.5+ .5 3.0+ 1.7		
			DK .3+ .2 89.3+ .1			AA .1+ .1 103.0			85.5		
			SI .3+ .2 97.0			A5 0.0+ 0.0 112.5			TOT 18.8+ 1.5 16.9+ 1.6		
			SU 1.9+ .5 4.3+ .7			TOT 98.3+ 8.6 141.8+ 13.2			72.5		
			SAP .2+ .1 17.0+ .0			36.0+ .0					
			PD .1+ .1 1.9+ 1.0			10+ 5.3+ .000					
			KD .3+ .2 95.5			10+ 2+ .0					
			SC 43.3+ 4.1 52.0+ 4.3			10+ 1.0					
			BI 1.3+ .5 3.6+ 1.6			82.5					
			EX 41.4+ 4.6 63.0+ .4			10+ 2					
			LV 1.2+ .4 9+ .3			10+ 4.2+ .0					
			97.0			10+ .5					
			WA 6.7+ .6 11.1+ .9			10+ 12.2+ .000					
			PP 0.0+ 0.0 112.5			10+ 0.0					
			DP 0.0+ 0.0 0.0+ 0.0			10+ 0.0					
			LS .1+ .1 103.0			10+ .4					
			A3 0.0+ 0.0 0.0+ 0.0			10+ 0.0					
			AA .1+ .1 103.0			10+ 1.0					
			A5 0.0+ 0.0 112.5			10+ 0.0					
			TOT 98.3+ 8.6 141.8+ 13.2			10+ 5.3+ .000					
			36.0+ .0			10+ 2+ .0					

SAE SOCIAL ATTENTION

	TEL	TR2
AT	36.0+ 3.6	14.3+ 1.6
SA	.86+ .6	13.5+ .3
AP	22.4+ 3.2	28.0+ 1.9
TU	3.1+ .6	1.7+ .4
TOT	60.3+ 4.2	23.1+ 3.2
	8.0+ .5	18.6+ .5

SCD SOCIAL CONTACT

	TEL	TR2
IM	8.1+ 2.5	21.3+ 3.9
HO	5.0+ 1.3	18.0+ .7
CR	0.0+ 0.0	11.4+ 3.0
SH	3.2+ 1.5	3.2+ 1.6
TOT	16.3+ 4.5	57.1+ 9.7
	27.0+ .5	12.6+ .5

SEX SEX-RELATED BEN

	TEL	TR2
PO	1.6+ .4	6.0+ 1.8
AM	0.0+ 0.0	3.7+ 2.1
MT	0.0+ 0.0	2.6+ 2.1
GC	0.0+ 0.0	9.0+ .8
PU	0.0+ 0.0	3.6+ .2
CO	0.0+ 0.0	97.3+ .1
PP	.3+ .2	81.0+ .3
TOT	1.9+ .4	16.7+ 5.4
	30.5+ .5	6.7+ .5

TOT 130.0+10.6 228.6+17.0
37.0+ .5

OTF OFFENSE

	TEL	TR2
TH	6.2+ 6	6+ .3
AK	1.9+ 6	2+ 1
BT	21.9+ 2.2	9.5+ 1.6
CH	2.0+ 4	0.0+ 0.0
AC	2+ 2	9+ 5
TOT	30.2+ 2.6	3.8+ 2.1
	5.0+ .5	19+ 20.4+ .5

OTA OFFENSIVE ANTI-VEHICLE

	TEL	TR2
OS	14.4+ 1.9	2.5+ 2.2
DU	3.4+ .6	13.0+ .2
PF	6.3+ 1.1	10.5+ .5
SP	.2+ .2	3.0+ .6
TOT	24.3+ 3.1	5.8+ 3.7
	18.0+ .5	15.6+ .5

DIA DISTANCE ANTI-VEHICLE

	TEL	TR2
ZZ	9.4+ 2.3	16.0+ .5
GL	7.4+ 1.8	5.9+ .4
WR	7.3+ 1.3	21.5+ .6
EA	7.2+ 1.7	13.0+ .9
TOT	31.3+ 4.6	2.8+ 2.5
	10.5+ .5	18.6+ .5

DIA DEFENSIVE ANTI-VEHICLE

	TEL	TR2
OS	4+ .4	1+ 1
UP	.7+ .3	10.2+ .2
DU	0.0+ 0.0	87.5+ .2
DS	0+ 0	106.0+ .2
TOT	1+ .5	3.4+ 3.7
	79.5+ .5	19+ 2.2

ARF ARRESTED FLIGHT

	TEL	TR2
CR	0.0+ 0.0	.4+ .5
FR	25.4+ 5.8	7.4+ 1.4
RK	0.0+ 0.0	31.5+ .1
SL	0.0+ 0.0	105.0+ .0
TOT	25.4+ 5.8	8.1+ 1.9
	35.5+ .5	10+ 10.2+ .5

ESC ESCAPE

	TEL	TR2
FG	.4+ .2	1.6+ .5
EV	0.0+ 0.0	56.5+ .9
RT	12.8+ 1.3	5.9+ .9
FL	0.0+ 0.0	29.0+ .1
ON	5.1+ 1.7	14.9+ .7
TOT	18.3+ 1.8	26.5+ 4.7
	29.3+ .4	19+ .4

EXPERIMENT : GBSA			SAT SOCIAL ATTENTION			OFF OFFENSE			DIA DEFENSIVE AMBIVALENCE		
NUMBER OF TREATMENTS : 2			TRI			TRI			TRI		
TREATMENT 1 (TRI) : CONTROL			TRI			TRI			TRI		
NUMBER OF ENCOUNTERS : 8			TRI			TRI			TRI		
TREATMENT 2 (TR2) : OLF-OLF+2.0			TRI			TRI			TRI		
NUMBER OF ENCOUNTERS : 8			TRI			TRI			TRI		
TOTAL FREQUENCY			TRI			TRI			TRI		
NDO NON-SOCIAL			TRI			TRI			TRI		
SC 0.0+0.0			1.1	1.1	1.1	1.1	1.1	1.1	0.0	0.0	0.0
SR 1.1+1.1			2.0	2.0	2.0	2.0	2.0	2.0	0.0	0.0	0.0
SH 0.0+0.0			1.6	1.6	1.6	1.6	1.6	1.6	0.0	0.0	0.0
JP 1.1+1.1			2.0	2.0	2.0	2.0	2.0	2.0	0.0	0.0	0.0
EA 0.0+0.0			1.1	1.1	1.1	1.1	1.1	1.1	0.0	0.0	0.0
DK 1.1+1.1			2.0	2.0	2.0	2.0	2.0	2.0	0.0	0.0	0.0
SI 0.0+0.0			0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
SU 1.8+1.8			4.1	4.1	4.1	4.1	4.1	4.1	0.0	0.0	0.0
SAP 1.1+1.1			1.5	1.5	1.5	1.5	1.5	1.5	0.0	0.0	0.0
PD 1.1+1.1			1.5	1.5	1.5	1.5	1.5	1.5	0.0	0.0	0.0
AD 1.1+1.1			1.5	1.5	1.5	1.5	1.5	1.5	0.0	0.0	0.0
SC 4.8+4.8			6.2	6.2	6.2	6.2	6.2	6.2	0.0	0.0	0.0
DI 1.1+1.1			1.5	1.5	1.5	1.5	1.5	1.5	0.0	0.0	0.0
EX 4.8+4.8			5.5	5.5	5.5	5.5	5.5	5.5	0.0	0.0	0.0
LV 1.8+1.8			4.1	4.1	4.1	4.1	4.1	4.1	0.0	0.0	0.0
JA 6.0+6.0			1.1	1.1	1.1	1.1	1.1	1.1	0.0	0.0	0.0
FP 0.0+0.0			0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
DF 0.0+0.0			0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
LS 1.1+1.1			2.0	2.0	2.0	2.0	2.0	2.0	0.0	0.0	0.0
AJ 0.0+0.0			0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
AC 0.0+0.0			0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
AS 0.0+0.0			0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
TOT 108.4+118.1			115.5	115.5	115.5	115.5	115.5	115.5	0.0	0.0	0.0
SC 0.0+0.0			1.1	1.1	1.1	1.1	1.1	1.1	0.0	0.0	0.0
SR 1.1+1.1			2.0	2.0	2.0	2.0	2.0	2.0	0.0	0.0	0.0
SH 0.0+0.0			1.6	1.6	1.6	1.6	1.6	1.6	0.0	0.0	0.0
JP 1.1+1.1			2.0	2.0	2.0	2.0	2.0	2.0	0.0	0.0	0.0
EA 0.0+0.0			1.1	1.1	1.1	1.1	1.1	1.1	0.0	0.0	0.0
DK 1.1+1.1			2.0	2.0	2.0	2.0	2.0	2.0	0.0	0.0	0.0
SI 0.0+0.0			0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
SU 1.8+1.8			4.1	4.1	4.1	4.1	4.1	4.1	0.0	0.0	0.0
SAP 1.1+1.1			1.5	1.5	1.5	1.5	1.5	1.5	0.0	0.0	0.0
PD 1.1+1.1			1.5	1.5	1.5	1.5	1.5	1.5	0.0	0.0	0.0
AD 1.1+1.1			1.5	1.5	1.5	1.5	1.5	1.5	0.0	0.0	0.0
SC 4.8+4.8			6.2	6.2	6.2	6.2	6.2	6.2	0.0	0.0	0.0
DI 1.1+1.1			1.5	1.5	1.5	1.5	1.5	1.5	0.0	0.0	0.0
EX 4.8+4.8			5.5	5.5	5.5	5.5	5.5	5.5	0.0	0.0	0.0
LV 1.8+1.8			4.1	4.1	4.1	4.1	4.1	4.1	0.0	0.0	0.0
JA 6.0+6.0			1.1	1.1	1.1	1.1	1.1	1.1	0.0	0.0	0.0
FP 0.0+0.0			0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
DF 0.0+0.0			0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
LS 1.1+1.1			2.0	2.0	2.0	2.0	2.0	2.0	0.0	0.0	0.0
AJ 0.0+0.0			0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
AC 0.0+0.0			0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
AS 0.0+0.0			0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
TOT 108.4+118.1			115.5	115.5	115.5	115.5	115.5	115.5	0.0	0.0	0.0
SC 0.0+0.0			1.1	1.1	1.1	1.1	1.1	1.1	0.0	0.0	0.0
SR 1.1+1.1			2.0	2.0	2.0	2.0	2.0	2.0	0.0	0.0	0.0
SH 0.0+0.0			1.6	1.6	1.6	1.6	1.6	1.6	0.0	0.0	0.0
JP 1.1+1.1			2.0	2.0	2.0	2.0	2.0	2.0	0.0	0.0	0.0
EA 0.0+0.0			1.1	1.1	1.1	1.1	1.1	1.1	0.0	0.0	0.0
DK 1.1+1.1			2.0	2.0	2.0	2.0	2.0	2.0	0.0	0.0	0.0
SI 0.0+0.0			0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
SU 1.8+1.8			4.1	4.1	4.1	4.1	4.1	4.1	0.0	0.0	0.0
SAP 1.1+1.1			1.5	1.5	1.5	1.5	1.5	1.5	0.0	0.0	0.0
PD 1.1+1.1			1.5	1.5	1.5	1.5	1.5	1.5	0.0	0.0	0.0
AD 1.1+1.1			1.5	1.5	1.5	1.5	1.5	1.5	0.0	0.0	0.0
SC 4.8+4.8			6.2	6.2	6.2	6.2	6.2	6.2	0.0	0.0	0.0
DI 1.1+1.1			1.5	1.5	1.5	1.5	1.5	1.5	0.0	0.0	0.0
EX 4.8+4.8			5.5	5.5	5.5	5.5	5.5	5.5	0.0	0.0	0.0
LV 1.8+1.8			4.1	4.1	4.1	4.1	4.1	4.1	0.0	0.0	0.0
JA 6.0+6.0			1.1	1.1	1.1	1.1	1.1	1.1	0.0	0.0	0.0
FP 0.0+0.0			0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
DF 0.0+0.0			0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
LS 1.1+1.1			2.0	2.0	2.0	2.0	2.0	2.0	0.0	0.0	0.0
AJ 0.0+0.0			0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
AC 0.0+0.0			0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
AS 0.0+0.0			0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
TOT 108.4+118.1			115.5	115.5	115.5	115.5	115.5	115.5	0.0	0.0	0.0

SAT SOCIAL ATTENTION

	TRI	TR2
AT 31.3+3.7	20.9+3.7	M= 2.8 #
SA .8+ .2	16.0	M= 0.0
AP 22.9+2.3	20.0+4.5	M= 1.6
TU 1.5+ .4	1.0+ .3	M= .5

TOT 56.0+6.6 38.3+7.4
M= 2.8 #

SOC SOCIAL CONTACT

	TRI	TR2
TH 11.2+3.4	22.3+6.3	M= 1.3
MO 6.8+1.6	12.1+6.9	M= 3.2 #
CR 0.0+0.0	6.8+3.4	M= 8.4 #
SH 2.3+1.1	3.7+1.3	M= .4
TOT 20.3+5.4	55.1+17.0	M= 1.6

SEX SEX-RELATED GEN

	TRI	TR2
PO 1.2+ .5	1.9+1.8	M= 1.8
AM 0.0+0.0	2.0+2.0	M= 1.0
MT 0.0+0.0	0.0+0.0	M= 0.0
GC 0.0+0.0	0.0+0.0	M= 0.0
PU 0.0+0.0	1.1+1.1	M= 1.0
CO 0.0+0.0	3.2+0.0	M= 0.0
PF 0.0+0.0	1.0+1.5	M= 0.0
TOT 1.2+ .5	6.8+3.7	M= 4.0 #

NAME	DURATION
MSO NON-SOCIAL	

	TRI	TR2
SC 0.0+0.0	1+ .1	M= 1.0
SR 1+ .1	28.0+3+ .2	M= .4
SH 0.0+0.0	4+ .2	M= 4.9 #
JP 1+ .1	16.0	M= .6
EA 0.0+0.0	1+ .1	M= 1.0
DK 1+ .1	31.1+ .1	M= .0
SI 0.0+0.0	0.0+0.0	M= 0.0
SU 1.8+ .6	4.8+1.2	M= 3.8 #
SAP 1+ .1	2.8+1.1	M= 12.3 #
PD 1+ .1	3.0+1.3	M= 2.8
KD 1+ .1	19.0+ .2	M= 1.7
SC 78.2+11.4	67.9+12.0	M= .6
DI 7+ .5	18.4+2.2	M= 3.2 #
EX 65.9+7.4	77.8+9.9	M= 0
LV 8+ .2	31.0	M= 3.2 #
UA 7.6+1.6	10.0+1.6	M= 1.3
FP 0.0+0.0	0.0+0.0	M= 0.0
DP 0.0+0.0	32.0	M= 0.0
LS 1+ .1	1.0+0.0	M= 1.0
A3 0.0+0.0	28.0	M= 0.0
A6 0.0+0.0	30.0+0.0	M= 0.0
A5 0.0+0.0	32.0	M= 0.0
TOT 153.7+16.1	170.2+23.6	M= .1

OFF OFFENSE

	TRI	TR2
TH 5.6+ .9	2.9+1.4	M= 2.7
AK 1.4+ .5	13.5+ .4	M= 4.3 #
BT 19.8+4.6	21.5+4.9	M= 1.7
CH 1.1+ .4	4+ .2	M= 1.2
AC 0.0+0.0	18.5+ .3	M= 4.9 #
TOT 28.0+6.1	55.8+6.3	M= 1.9

OFF OFFENSIVE AMBIVALENCE

	TRI	TR2
OS 8.7+2.4	6.4+3.3	M= .2
OU 4.5+1.0	3.4+1.6	M= .9
PI 8.4+2.6	7.4+3.1	M= .9
SP 0.0+0.0	0.0+0.0	M= 0.0
TOT 21.6+5.4	19.4+7.6	M= .5

DIA DISTANCE AMBIVALENCE

	TRI	TR2
ZZ 8.1+1.5	3.1+1.7	M= 4.0 #
CI 7.0+3.8	3.4+2.3	M= .0
WR 6.3+2.4	6.9+3.4	M= 0.0
RA 5.8+1.5	32.0	M= 4.3 #
TOT 30.2+7.1	48.9+6.8	M= 1.3

HWA HWA-SENSITIVE AMBIVALENCE

	TRI	TR2
OR 0.0+0.0	0.0+0.0	M= 0.0
UT 0.0+0.0	0.0+0.0	M= 0.0
DU 0.0+0.0	28.2+ .2	M= 1.0
HS 0.0+0.0	0.0+0.0	M= 0.0
TOT 0.0+0.0	28.2	M= 1.0

ARF ARRESTED FLIGHT

	TRI	TR2
CR 0.0+0.0	1.2+1.1	M= 2.1
TR 19.0+2.4	11.1+2.8	M= 3.6 #
KZ 0.0+0.0	0.0+0.0	M= 0.0
SL 0.0+0.0	0.0+0.0	M= 0.0
TOT 19.0+2.4	12.3+3.0	M= 2.5

ESC ESCAPE

	TRI	TR2
PC 1+ .1	16.4+ .2	M= 3.7 #
EV 0.0+0.0	16.9+ .6	M= 3.4 #
FL 16.0+1.2	11.0+1.6	M= 2.0
FL 0.0+0.0	32.0	M= 0.0
OM 10.2+3.9	4.0+3.4	M= .9
TOT 26.3+4.0	20.5+4.9	M= 1.1

TREATMENT : AFCA			SAT SOCIAL ATTENTION			OFF OFFENSE			DEA DEFENSIVE AMBIVALENCE		
NUMBER OF TREATMENTS : 2			TREATMENT 1 (TEL) : CONTROL			TREATMENT 2 (TEL) : ACQU-DEP			TREATMENT 1 (TEL) : CONTROL		
NUMBER OF ENCOUNTERS : 10			NUMBER OF ENCOUNTERS : 15			NUMBER OF ENCOUNTERS : 15			NUMBER OF ENCOUNTERS : 15		
FREQUENCY			FREQUENCY			FREQUENCY			FREQUENCY		
NED NON-SOCIAL			NED NON-SOCIAL			NED NON-SOCIAL			NED NON-SOCIAL		
TEL	TR2		TEL	TR2		TEL	TR2		TEL	TR2	
SC	4.2	1.1+ .6	SC	4.2	1.1+ .6	AT	20.2+ 1.7	8.5+ .7	TH	2.5+ .4	1.9+ .5
SR	2.1	92.0	SR	2.1	92.0	SA	1.4	1.1+ .1	AK	9+ .4	45.0
SH	0.0+ 0.0	1.1+ .1	SH	0.0+ 0.0	1.1+ .1	AP	13.4+ 1.1	31.5+ 1.2	ST	22.5+ 3.2	100.0
JP	1.1+ .1	117.1+ .1	JP	1.1+ .1	117.1+ .1	TU	7.4+ 1.2	5.0+ .8	DS	0.0+ 0.0	1.1+ .1
EA	1.1+ .1	117.1+ .1	EA	1.1+ .1	117.1+ .1		82.0		AC	1.1+ .6	113.0
OK	7.6	119.0	OK	7.6	119.0	TOT	43.1+ 3.1	22.4+ 2.0	TOT	1.1+ .6	113.0
SI	1.1+ .1	94.3	SI	1.1+ .1	94.3		16.0		TOT	1.1+ .6	113.0
SU	6.2	92.0	SU	6.2	92.0		16.0				
SAP	2.1	1.5+ .6	SAP	2.1	1.5+ .6		16.0				
PD	1.1+ .1	117.1+ .1	PD	1.1+ .1	117.1+ .1		16.0				
KD	0.0+ 0.0	1.1+ .1	KD	0.0+ 0.0	1.1+ .1		16.0				
SC	29.9+ 2.6	30.8+ 2.4	SC	29.9+ 2.6	30.8+ 2.4		101.0				
DI	6.2	110.0	DI	6.2	110.0		101.0				
EX	37.5+ 2.9	41.5+ 3.5	EX	37.5+ 2.9	41.5+ 3.5		101.0				
LV	2.3+ .4	1.1+ .2	LV	2.3+ .4	1.1+ .2		101.0				
VA	5.1+ .7	81.5+ .9	VA	5.1+ .7	81.5+ .9		101.0				
FP	0.0+ 0.0	0.0+ 0.0	FP	0.0+ 0.0	0.0+ 0.0		101.0				
OP	0.0+ 0.0	0.0+ 0.0	OP	0.0+ 0.0	0.0+ 0.0		101.0				
LS	1.1+ .1	84.0	LS	1.1+ .1	84.0		101.0				
AJ	6.2	110.0	AJ	6.2	110.0		101.0				
A6	0.0+ 0.0	0.0+ 0.0	A6	0.0+ 0.0	0.0+ 0.0		101.0				
A5	0.0+ 0.0	0.0+ 0.0	A5	0.0+ 0.0	0.0+ 0.0		101.0				
TOT	78.4+ 4.2	88.2+ 5.7	TOT	78.4+ 4.2	88.2+ 5.7		85.5				
		85.5			85.5						
SOCIAL CONTACT			SOCIAL CONTACT			SOCIAL CONTACT			SOCIAL CONTACT		
TEL	TR2		TEL	TR2		TEL	TR2		TEL	TR2	
IM	12.3+ 2.5	6.8+ 1.1	IM	12.3+ 2.5	6.8+ 1.1	OS	37.2+ 3.9	32.1+ 3.4	CR	0.0+ 0.0	1.1+ .1
NO	7.1+ 1.9	41.0	NO	7.1+ 1.9	41.0	OU	8.1+ 1.0	7.4+ 1.2	PK	15.1+ 1.6	118.2+ 1.7
OR	8.4	110.0	OR	8.4	110.0	PP	5.6+ .8	4.8+ 1.0	KE	0.0+ 0.0	0.0+ 0.0
SM	3.7+ 1.0	97.5	SM	3.7+ 1.0	97.5	SP	0.0+ 0.0	10.0	SL	0.0+ 0.0	0.0+ 0.0
TOT	23.8+ 5.5	34.3+ 2.3	TOT	23.8+ 5.5	34.3+ 2.3		101.0		TOT	15.1+ 1.6	118.2+ 1.7
		101.0			101.0						
SEX SEX-RELATED BUI			SEX SEX-RELATED BUI			SEX SEX-RELATED BUI			SEX SEX-RELATED BUI		
TEL	TR2		TEL	TR2		TEL	TR2		TEL	TR2	
FO	3.5+ 1.1	1.4+ .5	FO	3.5+ 1.1	1.4+ .5	ZZ	1.5+ .6	1.5+ .5	PC	3.5+ .6	3.5+ .3
AM	0.0+ 0.0	0.0+ 0.0	AM	0.0+ 0.0	0.0+ 0.0	CI	7.1+ 1.0	7.2+ 1.4	EV	3.5+ .6	111.5
MT	0.0+ 0.0	0.0+ 0.0	MT	0.0+ 0.0	0.0+ 0.0	VR	10.0+ 2.3	11.6+ 1.8	RT	18.0+ 1.6	15.1+ 1.7
CG	0.0+ 0.0	0.0+ 0.0	CG	0.0+ 0.0	0.0+ 0.0	BA	7.8+ 2.8	6.4+ 1.4	FL	1.1+ .1	89.0
PU	2.1+ .1	101.1+ .1	PU	2.1+ .1	101.1+ .1		110.0		OW	1.9+ .7	117.0
CO	1.1+ .1	101.1+ .1	CO	1.1+ .1	101.1+ .1		110.0		TOT	20.8+ 1.4	17.7+ 2.0
PF	0.0+ 0.0	0.0+ 0.0	PF	0.0+ 0.0	0.0+ 0.0		117.5				
TOT	3.8+ 1.2	1.5+ .5	TOT	3.8+ 1.2	1.5+ .5						
		85.5			85.5						
AFF ARRESTED FLIGHT			AFF ARRESTED FLIGHT			AFF ARRESTED FLIGHT			AFF ARRESTED FLIGHT		
TEL	TR2		TEL	TR2		TEL	TR2		TEL	TR2	
CR	0.0+ 0.0	1.1+ .1	CR	0.0+ 0.0	1.1+ .1	OS	37.2+ 3.9	32.1+ 3.4	PK	15.1+ 1.6	118.2+ 1.7
PK	15.1+ 1.6	118.2+ 1.7	PK	15.1+ 1.6	118.2+ 1.7	OU	8.1+ 1.0	7.4+ 1.2	KE	0.0+ 0.0	0.0+ 0.0
KE	0.0+ 0.0	0.0+ 0.0	KE	0.0+ 0.0	0.0+ 0.0	PP	5.6+ .8	4.8+ 1.0	SL	0.0+ 0.0	0.0+ 0.0
SL	0.0+ 0.0	0.0+ 0.0	SL	0.0+ 0.0	0.0+ 0.0	SP	0.0+ 0.0	10.0	TOT	15.1+ 1.6	118.2+ 1.7
TOT	15.1+ 1.6	118.2+ 1.7	TOT	15.1+ 1.6	118.2+ 1.7		101.0				
		86.5			86.5						
ESC ESCAPE			ESC ESCAPE			ESC ESCAPE			ESC ESCAPE		
TEL	TR2		TEL	TR2		TEL	TR2		TEL	TR2	
PC	3.5+ .6	3.5+ .3	PC	3.5+ .6	3.5+ .3	ZZ	1.5+ .6	1.5+ .5	EV	3.5+ .6	111.5
EV	3.5+ .6	111.5	EV	3.5+ .6	111.5	CI	7.1+ 1.0	7.2+ 1.4	RT	18.0+ 1.6	15.1+ 1.7
RT	18.0+ 1.6	15.1+ 1.7	RT	18.0+ 1.6	15.1+ 1.7	VR	10.0+ 2.3	11.6+ 1.8	FL	1.1+ .1	89.0
FL	1.1+ .1	89.0	FL	1.1+ .1	89.0	BA	7.8+ 2.8	6.4+ 1.4	OW	1.9+ .7	117.0
OW	1.9+ .7	117.0	OW	1.9+ .7	117.0		110.0		TOT	20.8+ 1.4	17.7+ 2.0
TOT	20.8+ 1.4	17.7+ 2.0	TOT	20.8+ 1.4	17.7+ 2.0		117.5				
		81.0			81.0						

[illegible]

EXPERIMENT : WACA				SAT SOCIAL ATTENTION				OFF OFFENSE				UPA DEFENSIVE AVOIDANCE			
NUMBER OF TREATMENTS : 2				TREATMENT 1 (TRI) : CONTROL				TREATMENT 2 (TR2)				TREATMENT 3 (TR3)			
NUMBER OF ENCOUNTERS : 16				TREATMENT 3 (TR3) : VIS-DEF				TREATMENT 4 (TR4) : VIS-DEF				TREATMENT 5 (TR5) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 6 (TR6) : VIS-DEF				TREATMENT 7 (TR7) : VIS-DEF				TREATMENT 8 (TR8) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 9 (TR9) : VIS-DEF				TREATMENT 10 (TR10) : VIS-DEF				TREATMENT 11 (TR11) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 12 (TR12) : VIS-DEF				TREATMENT 13 (TR13) : VIS-DEF				TREATMENT 14 (TR14) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 15 (TR15) : VIS-DEF				TREATMENT 16 (TR16) : VIS-DEF				TREATMENT 17 (TR17) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 18 (TR18) : VIS-DEF				TREATMENT 19 (TR19) : VIS-DEF				TREATMENT 20 (TR20) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 21 (TR21) : VIS-DEF				TREATMENT 22 (TR22) : VIS-DEF				TREATMENT 23 (TR23) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 24 (TR24) : VIS-DEF				TREATMENT 25 (TR25) : VIS-DEF				TREATMENT 26 (TR26) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 27 (TR27) : VIS-DEF				TREATMENT 28 (TR28) : VIS-DEF				TREATMENT 29 (TR29) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 30 (TR30) : VIS-DEF				TREATMENT 31 (TR31) : VIS-DEF				TREATMENT 32 (TR32) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 33 (TR33) : VIS-DEF				TREATMENT 34 (TR34) : VIS-DEF				TREATMENT 35 (TR35) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 36 (TR36) : VIS-DEF				TREATMENT 37 (TR37) : VIS-DEF				TREATMENT 38 (TR38) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 39 (TR39) : VIS-DEF				TREATMENT 40 (TR40) : VIS-DEF				TREATMENT 41 (TR41) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 42 (TR42) : VIS-DEF				TREATMENT 43 (TR43) : VIS-DEF				TREATMENT 44 (TR44) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 45 (TR45) : VIS-DEF				TREATMENT 46 (TR46) : VIS-DEF				TREATMENT 47 (TR47) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 48 (TR48) : VIS-DEF				TREATMENT 49 (TR49) : VIS-DEF				TREATMENT 50 (TR50) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 51 (TR51) : VIS-DEF				TREATMENT 52 (TR52) : VIS-DEF				TREATMENT 53 (TR53) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 54 (TR54) : VIS-DEF				TREATMENT 55 (TR55) : VIS-DEF				TREATMENT 56 (TR56) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 57 (TR57) : VIS-DEF				TREATMENT 58 (TR58) : VIS-DEF				TREATMENT 59 (TR59) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 60 (TR60) : VIS-DEF				TREATMENT 61 (TR61) : VIS-DEF				TREATMENT 62 (TR62) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 63 (TR63) : VIS-DEF				TREATMENT 64 (TR64) : VIS-DEF				TREATMENT 65 (TR65) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 66 (TR66) : VIS-DEF				TREATMENT 67 (TR67) : VIS-DEF				TREATMENT 68 (TR68) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 69 (TR69) : VIS-DEF				TREATMENT 70 (TR70) : VIS-DEF				TREATMENT 71 (TR71) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 72 (TR72) : VIS-DEF				TREATMENT 73 (TR73) : VIS-DEF				TREATMENT 74 (TR74) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 75 (TR75) : VIS-DEF				TREATMENT 76 (TR76) : VIS-DEF				TREATMENT 77 (TR77) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 78 (TR78) : VIS-DEF				TREATMENT 79 (TR79) : VIS-DEF				TREATMENT 80 (TR80) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 81 (TR81) : VIS-DEF				TREATMENT 82 (TR82) : VIS-DEF				TREATMENT 83 (TR83) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 84 (TR84) : VIS-DEF				TREATMENT 85 (TR85) : VIS-DEF				TREATMENT 86 (TR86) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 87 (TR87) : VIS-DEF				TREATMENT 88 (TR88) : VIS-DEF				TREATMENT 89 (TR89) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 90 (TR90) : VIS-DEF				TREATMENT 91 (TR91) : VIS-DEF				TREATMENT 92 (TR92) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 93 (TR93) : VIS-DEF				TREATMENT 94 (TR94) : VIS-DEF				TREATMENT 95 (TR95) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 96 (TR96) : VIS-DEF				TREATMENT 97 (TR97) : VIS-DEF				TREATMENT 98 (TR98) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 99 (TR99) : VIS-DEF				TREATMENT 100 (TR100) : VIS-DEF				TREATMENT 101 (TR101) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 102 (TR102) : VIS-DEF				TREATMENT 103 (TR103) : VIS-DEF				TREATMENT 104 (TR104) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 105 (TR105) : VIS-DEF				TREATMENT 106 (TR106) : VIS-DEF				TREATMENT 107 (TR107) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 108 (TR108) : VIS-DEF				TREATMENT 109 (TR109) : VIS-DEF				TREATMENT 110 (TR110) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 111 (TR111) : VIS-DEF				TREATMENT 112 (TR112) : VIS-DEF				TREATMENT 113 (TR113) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 114 (TR114) : VIS-DEF				TREATMENT 115 (TR115) : VIS-DEF				TREATMENT 116 (TR116) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 117 (TR117) : VIS-DEF				TREATMENT 118 (TR118) : VIS-DEF				TREATMENT 119 (TR119) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 120 (TR120) : VIS-DEF				TREATMENT 121 (TR121) : VIS-DEF				TREATMENT 122 (TR122) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 123 (TR123) : VIS-DEF				TREATMENT 124 (TR124) : VIS-DEF				TREATMENT 125 (TR125) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 126 (TR126) : VIS-DEF				TREATMENT 127 (TR127) : VIS-DEF				TREATMENT 128 (TR128) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 129 (TR129) : VIS-DEF				TREATMENT 130 (TR130) : VIS-DEF				TREATMENT 131 (TR131) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 132 (TR132) : VIS-DEF				TREATMENT 133 (TR133) : VIS-DEF				TREATMENT 134 (TR134) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 135 (TR135) : VIS-DEF				TREATMENT 136 (TR136) : VIS-DEF				TREATMENT 137 (TR137) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 138 (TR138) : VIS-DEF				TREATMENT 139 (TR139) : VIS-DEF				TREATMENT 140 (TR140) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 141 (TR141) : VIS-DEF				TREATMENT 142 (TR142) : VIS-DEF				TREATMENT 143 (TR143) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 144 (TR144) : VIS-DEF				TREATMENT 145 (TR145) : VIS-DEF				TREATMENT 146 (TR146) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 147 (TR147) : VIS-DEF				TREATMENT 148 (TR148) : VIS-DEF				TREATMENT 149 (TR149) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 150 (TR150) : VIS-DEF				TREATMENT 151 (TR151) : VIS-DEF				TREATMENT 152 (TR152) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 153 (TR153) : VIS-DEF				TREATMENT 154 (TR154) : VIS-DEF				TREATMENT 155 (TR155) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 156 (TR156) : VIS-DEF				TREATMENT 157 (TR157) : VIS-DEF				TREATMENT 158 (TR158) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 159 (TR159) : VIS-DEF				TREATMENT 160 (TR160) : VIS-DEF				TREATMENT 161 (TR161) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 162 (TR162) : VIS-DEF				TREATMENT 163 (TR163) : VIS-DEF				TREATMENT 164 (TR164) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 165 (TR165) : VIS-DEF				TREATMENT 166 (TR166) : VIS-DEF				TREATMENT 167 (TR167) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 168 (TR168) : VIS-DEF				TREATMENT 169 (TR169) : VIS-DEF				TREATMENT 170 (TR170) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 171 (TR171) : VIS-DEF				TREATMENT 172 (TR172) : VIS-DEF				TREATMENT 173 (TR173) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 174 (TR174) : VIS-DEF				TREATMENT 175 (TR175) : VIS-DEF				TREATMENT 176 (TR176) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 177 (TR177) : VIS-DEF				TREATMENT 178 (TR178) : VIS-DEF				TREATMENT 179 (TR179) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 180 (TR180) : VIS-DEF				TREATMENT 181 (TR181) : VIS-DEF				TREATMENT 182 (TR182) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 183 (TR183) : VIS-DEF				TREATMENT 184 (TR184) : VIS-DEF				TREATMENT 185 (TR185) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 186 (TR186) : VIS-DEF				TREATMENT 187 (TR187) : VIS-DEF				TREATMENT 188 (TR188) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 189 (TR189) : VIS-DEF				TREATMENT 190 (TR190) : VIS-DEF				TREATMENT 191 (TR191) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 192 (TR192) : VIS-DEF				TREATMENT 193 (TR193) : VIS-DEF				TREATMENT 194 (TR194) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 195 (TR195) : VIS-DEF				TREATMENT 196 (TR196) : VIS-DEF				TREATMENT 197 (TR197) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 198 (TR198) : VIS-DEF				TREATMENT 199 (TR199) : VIS-DEF				TREATMENT 200 (TR200) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 201 (TR201) : VIS-DEF				TREATMENT 202 (TR202) : VIS-DEF				TREATMENT 203 (TR203) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 204 (TR204) : VIS-DEF				TREATMENT 205 (TR205) : VIS-DEF				TREATMENT 206 (TR206) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 207 (TR207) : VIS-DEF				TREATMENT 208 (TR208) : VIS-DEF				TREATMENT 209 (TR209) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 210 (TR210) : VIS-DEF				TREATMENT 211 (TR211) : VIS-DEF				TREATMENT 212 (TR212) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 213 (TR213) : VIS-DEF				TREATMENT 214 (TR214) : VIS-DEF				TREATMENT 215 (TR215) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 216 (TR216) : VIS-DEF				TREATMENT 217 (TR217) : VIS-DEF				TREATMENT 218 (TR218) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 219 (TR219) : VIS-DEF				TREATMENT 220 (TR220) : VIS-DEF				TREATMENT 221 (TR221) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 222 (TR222) : VIS-DEF				TREATMENT 223 (TR223) : VIS-DEF				TREATMENT 224 (TR224) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 225 (TR225) : VIS-DEF				TREATMENT 226 (TR226) : VIS-DEF				TREATMENT 227 (TR227) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 228 (TR228) : VIS-DEF				TREATMENT 229 (TR229) : VIS-DEF				TREATMENT 230 (TR230) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 231 (TR231) : VIS-DEF				TREATMENT 232 (TR232) : VIS-DEF				TREATMENT 233 (TR233) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 234 (TR234) : VIS-DEF				TREATMENT 235 (TR235) : VIS-DEF				TREATMENT 236 (TR236) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 237 (TR237) : VIS-DEF				TREATMENT 238 (TR238) : VIS-DEF				TREATMENT 239 (TR239) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 240 (TR240) : VIS-DEF				TREATMENT 241 (TR241) : VIS-DEF				TREATMENT 242 (TR242) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 243 (TR243) : VIS-DEF				TREATMENT 244 (TR244) : VIS-DEF				TREATMENT 245 (TR245) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 246 (TR246) : VIS-DEF				TREATMENT 247 (TR247) : VIS-DEF				TREATMENT 248 (TR248) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 249 (TR249) : VIS-DEF				TREATMENT 250 (TR250) : VIS-DEF				TREATMENT 251 (TR251) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 252 (TR252) : VIS-DEF				TREATMENT 253 (TR253) : VIS-DEF				TREATMENT 254 (TR254) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 255 (TR255) : VIS-DEF				TREATMENT 256 (TR256) : VIS-DEF				TREATMENT 257 (TR257) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 258 (TR258) : VIS-DEF				TREATMENT 259 (TR259) : VIS-DEF				TREATMENT 260 (TR260) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 261 (TR261) : VIS-DEF				TREATMENT 262 (TR262) : VIS-DEF				TREATMENT 263 (TR263) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 264 (TR264) : VIS-DEF				TREATMENT 265 (TR265) : VIS-DEF				TREATMENT 266 (TR266) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 267 (TR267) : VIS-DEF				TREATMENT 268 (TR268) : VIS-DEF				TREATMENT 269 (TR269) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 270 (TR270) : VIS-DEF				TREATMENT 271 (TR271) : VIS-DEF				TREATMENT 272 (TR272) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 273 (TR273) : VIS-DEF				TREATMENT 274 (TR274) : VIS-DEF				TREATMENT 275 (TR275) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 276 (TR276) : VIS-DEF				TREATMENT 277 (TR277) : VIS-DEF				TREATMENT 278 (TR278) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 279 (TR279) : VIS-DEF				TREATMENT 280 (TR280) : VIS-DEF				TREATMENT 281 (TR281) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 282 (TR282) : VIS-DEF				TREATMENT 283 (TR283) : VIS-DEF				TREATMENT 284 (TR284) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 285 (TR285) : VIS-DEF				TREATMENT 286 (TR286) : VIS-DEF				TREATMENT 287 (TR287) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 288 (TR288) : VIS-DEF				TREATMENT 289 (TR289) : VIS-DEF				TREATMENT 290 (TR290) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 291 (TR291) : VIS-DEF				TREATMENT 292 (TR292) : VIS-DEF				TREATMENT 293 (TR293) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 294 (TR294) : VIS-DEF				TREATMENT 295 (TR295) : VIS-DEF				TREATMENT 296 (TR296) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 297 (TR297) : VIS-DEF				TREATMENT 298 (TR298) : VIS-DEF				TREATMENT 299 (TR299) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 300 (TR300) : VIS-DEF				TREATMENT 301 (TR301) : VIS-DEF				TREATMENT 302 (TR302) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 303 (TR303) : VIS-DEF				TREATMENT 304 (TR304) : VIS-DEF				TREATMENT 305 (TR305) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 306 (TR306) : VIS-DEF				TREATMENT 307 (TR307) : VIS-DEF				TREATMENT 308 (TR308) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 309 (TR309) : VIS-DEF				TREATMENT 310 (TR310) : VIS-DEF				TREATMENT 311 (TR311) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 312 (TR312) : VIS-DEF				TREATMENT 313 (TR313) : VIS-DEF				TREATMENT 314 (TR314) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 315 (TR315) : VIS-DEF				TREATMENT 316 (TR316) : VIS-DEF				TREATMENT 317 (TR317) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 318 (TR318) : VIS-DEF				TREATMENT 319 (TR319) : VIS-DEF				TREATMENT 320 (TR320) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 321 (TR321) : VIS-DEF				TREATMENT 322 (TR322) : VIS-DEF				TREATMENT 323 (TR323) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 324 (TR324) : VIS-DEF				TREATMENT 325 (TR325) : VIS-DEF				TREATMENT 326 (TR326) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 327 (TR327) : VIS-DEF				TREATMENT 328 (TR328) : VIS-DEF				TREATMENT 329 (TR329) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 330 (TR330) : VIS-DEF				TREATMENT 331 (TR331) : VIS-DEF				TREATMENT 332 (TR332) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 333 (TR333) : VIS-DEF				TREATMENT 334 (TR334) : VIS-DEF				TREATMENT 335 (TR335) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 336 (TR336) : VIS-DEF				TREATMENT 337 (TR337) : VIS-DEF				TREATMENT 338 (TR338) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 339 (TR339) : VIS-DEF				TREATMENT 340 (TR340) : VIS-DEF				TREATMENT 341 (TR341) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 342 (TR342) : VIS-DEF				TREATMENT 343 (TR343) : VIS-DEF				TREATMENT 344 (TR344) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 345 (TR345) : VIS-DEF				TREATMENT 346 (TR346) : VIS-DEF				TREATMENT 347 (TR347) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 348 (TR348) : VIS-DEF				TREATMENT 349 (TR349) : VIS-DEF				TREATMENT 350 (TR350) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 351 (TR351) : VIS-DEF				TREATMENT 352 (TR352) : VIS-DEF				TREATMENT 353 (TR353) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 354 (TR354) : VIS-DEF				TREATMENT 355 (TR355) : VIS-DEF				TREATMENT 356 (TR356) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 357 (TR357) : VIS-DEF				TREATMENT 358 (TR358) : VIS-DEF				TREATMENT 359 (TR359) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 360 (TR360) : VIS-DEF				TREATMENT 361 (TR361) : VIS-DEF				TREATMENT 362 (TR362) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 363 (TR363) : VIS-DEF				TREATMENT 364 (TR364) : VIS-DEF				TREATMENT 365 (TR365) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 366 (TR366) : VIS-DEF				TREATMENT 367 (TR367) : VIS-DEF				TREATMENT 368 (TR368) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 369 (TR369) : VIS-DEF				TREATMENT 370 (TR370) : VIS-DEF				TREATMENT 371 (TR371) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 372 (TR372) : VIS-DEF				TREATMENT 373 (TR373) : VIS-DEF				TREATMENT 374 (TR374) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 375 (TR375) : VIS-DEF				TREATMENT 376 (TR376) : VIS-DEF				TREATMENT 377 (TR377) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 378 (TR378) : VIS-DEF				TREATMENT 379 (TR379) : VIS-DEF				TREATMENT 380 (TR380) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 381 (TR381) : VIS-DEF				TREATMENT 382 (TR382) : VIS-DEF				TREATMENT 383 (TR383) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 384 (TR384) : VIS-DEF				TREATMENT 385 (TR385) : VIS-DEF				TREATMENT 386 (TR386) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 387 (TR387) : VIS-DEF				TREATMENT 388 (TR388) : VIS-DEF				TREATMENT 389 (TR389) : VIS-DEF			
NUMBER OF ENCOUNTERS : 16				TREATMENT 390 (TR390) : VIS-DEF				TREATMENT 391 (TR391) : VIS-DEF				TREATMENT 3			

SHT SOCIAL ATTENTION		OTF OFFENSE		HIA DEFENSIVE ARRIVALANCE	
NAME	DURATION	TR1	TR2	TR1	TR2
NSD NON SOCIAL					
AT	10.6	3.3	25.3	3.8	
EA	2.6	1.1	88.0		
AP	16.4	1.7	10.1	1.1	
TU	5.4	1.3	61.0		
TOT	32.5	4.7	41.7	4.7	
SOD SOCIAL CONTACT					
IM	18.2	4.5	25.4	5.4	
MO	5.8	1.7	8.2	2.1	
CR	8.0	3.1	1.5	6	
SH	2.6	1.1	6.3	1.3	
TOT	27.5	6.4	41.2	8.1	
SIX SEX RELATED BUI					
FO	1.5	0.6	1.9	0.7	
AN	0.0	0.0	105.3	0	
RT	1.6	1.1	0.0	0.0	
CC	0.0	0.0	0.0	0.0	
PU	0.0	0.0	120.8	5	
CO	0.0	0.0	0.0	0.0	
PP	2.0	1.1	0.0	0.0	
TOT	1.9	0.6	2.7	0.9	
SIX SEX RELATED BUI					
FO	1.5	0.6	1.9	0.7	
AN	0.0	0.0	120.0	0	
RT	1.6	1.1	0.0	0.0	
CC	0.0	0.0	0.0	0.0	
PU	0.0	0.0	120.8	5	
CO	0.0	0.0	0.0	0.0	
PP	2.0	1.1	0.0	0.0	
TOT	1.9	0.6	2.7	0.9	
SIX SEX RELATED BUI					
FO	1.5	0.6	1.9	0.7	
AN	0.0	0.0	120.0	0	
RT	1.6	1.1	0.0	0.0	
CC	0.0	0.0	0.0	0.0	
PU	0.0	0.0	120.8	5	
CO	0.0	0.0	0.0	0.0	
PP	2.0	1.1	0.0	0.0	
TOT	1.9	0.6	2.7	0.9	
SIX SEX RELATED BUI					
FO	1.5	0.6	1.9	0.7	
AN	0.0	0.0	120.0	0	
RT	1.6	1.1	0.0	0.0	
CC	0.0	0.0	0.0	0.0	
PU	0.0	0.0	120.8	5	
CO	0.0	0.0	0.0	0.0	
PP	2.0	1.1	0.0	0.0	
TOT	1.9	0.6	2.7	0.9	
SIX SEX RELATED BUI					
FO	1.5	0.6	1.9	0.7	
AN	0.0	0.0	120.0	0	
RT	1.6	1.1	0.0	0.0	
CC	0.0	0.0	0.0	0.0	
PU	0.0	0.0	120.8	5	
CO	0.0	0.0	0.0	0.0	
PP	2.0	1.1	0.0	0.0	
TOT	1.9	0.6	2.7	0.9	
SIX SEX RELATED BUI					
FO	1.5	0.6	1.9	0.7	
AN	0.0	0.0	120.0	0	
RT	1.6	1.1	0.0	0.0	
CC	0.0	0.0	0.0	0.0	
PU	0.0	0.0	120.8	5	
CO	0.0	0.0	0.0	0.0	
PP	2.0	1.1	0.0	0.0	
TOT	1.9	0.6	2.7	0.9	
SIX SEX RELATED BUI					
FO	1.5	0.6	1.9	0.7	
AN	0.0	0.0	120.0	0	
RT	1.6	1.1	0.0	0.0	
CC	0.0	0.0	0.0	0.0	
PU	0.0	0.0	120.8	5	
CO	0.0	0.0	0.0	0.0	
PP	2.0	1.1	0.0	0.0	
TOT	1.9	0.6	2.7	0.9	
SIX SEX RELATED BUI					
FO	1.5	0.6	1.9	0.7	
AN	0.0	0.0	120.0	0	
RT	1.6	1.1	0.0	0.0	
CC	0.0	0.0	0.0	0.0	
PU	0.0	0.0	120.8	5	
CO	0.0	0.0	0.0	0.0	
PP	2.0	1.1	0.0	0.0	
TOT	1.9	0.6	2.7	0.9	
SIX SEX RELATED BUI					
FO	1.5	0.6	1.9	0.7	
AN	0.0	0.0	120.0	0	
RT	1.6	1.1	0.0	0.0	
CC	0.0	0.0	0.0	0.0	
PU	0.0	0.0	120.8	5	
CO	0.0	0.0	0.0	0.0	
PP	2.0	1.1	0.0	0.0	
TOT	1.9	0.6	2.7	0.9	
SIX SEX RELATED BUI					
FO	1.5	0.6	1.9	0.7	
AN	0.0	0.0	120.0	0	
RT	1.6	1.1	0.0	0.0	
CC	0.0	0.0	0.0	0.0	
PU	0.0	0.0	120.8	5	
CO	0.0	0.0	0.0	0.0	
PP	2.0	1.1	0.0	0.0	
TOT	1.9	0.6	2.7	0.9	
SIX SEX RELATED BUI					
FO	1.5	0.6	1.9	0.7	
AN	0.0	0.0	120.0	0	
RT	1.6	1.1	0.0	0.0	
CC	0.0	0.0	0.0	0.0	
PU	0.0	0.0	120.8	5	
CO	0.0	0.0	0.0	0.0	
PP	2.0	1.1	0.0	0.0	
TOT	1.9	0.6	2.7	0.9	
SIX SEX RELATED BUI					
FO	1.5	0.6	1.9	0.7	
AN	0.0	0.0	120.0	0	
RT	1.6	1.1	0.0	0.0	
CC	0.0	0.0	0.0	0.0	
PU	0.0	0.0	120.8	5	
CO	0.0	0.0	0.0	0.0	
PP	2.0	1.1	0.0	0.0	
TOT	1.9	0.6	2.7	0.9	
SIX SEX RELATED BUI					
FO	1.5	0.6	1.9	0.7	
AN	0.0	0.0	120.0	0	
RT	1.6	1.1	0.0	0.0	
CC	0.0	0.0	0.0	0.0	
PU	0.0	0.0	120.8	5	
CO	0.0	0.0	0.0	0.0	
PP	2.0	1.1	0.0	0.0	
TOT	1.9	0.6	2.7	0.9	
SIX SEX RELATED BUI					
FO	1.5	0.6	1.9	0.7	
AN	0.0	0.0	120.0	0	
RT	1.6	1.1	0.0	0.0	
CC	0.0	0.0	0.0	0.0	
PU	0.0	0.0	120.8	5	
CO	0.0	0.0	0.0	0.0	
PP	2.0	1.1	0.0	0.0	
TOT	1.9	0.6	2.7	0.9	
SIX SEX RELATED BUI					
FO	1.5	0.6	1.9	0.7	
AN	0.0	0.0	120.0	0	
RT	1.6	1.1	0.0	0.0	
CC	0.0	0.0	0.0	0.0	
PU	0.0	0.0	120.8	5	
CO	0.0	0.0	0.0	0.0	
PP	2.0	1.1	0.0	0.0	
TOT	1.9	0.6	2.7	0.9	
SIX SEX RELATED BUI					
FO	1.5	0.6	1.9	0.7	
AN	0.0	0.0	120.0	0	
RT	1.6	1.1	0.0	0.0	
CC	0.0	0.0	0.0	0.0	
PU	0.0	0.0	120.8	5	
CO	0.0	0.0	0.0	0.0	
PP	2.0	1.1	0.0	0.0	
TOT	1.9	0.6	2.7	0.9	
SIX SEX RELATED BUI					
FO	1.5	0.6	1.9	0.7	
AN	0.0	0.0	120.0	0	
RT	1.6	1.1	0.0	0.0	
CC	0.0	0.0	0.0	0.0	
PU	0.0	0.0	120.8	5	
CO	0.0	0.0	0.0	0.0	
PP	2.0	1.1	0.0	0.0	
TOT	1.9	0.6	2.7	0.9	
SIX SEX RELATED BUI					
FO	1.5	0.6	1.9	0.7	
AN	0.0	0.0	120.0	0	
RT	1.6	1.1	0.0	0.0	
CC	0.0	0.0	0.0	0.0	
PU	0.0	0.0	120.8	5	
CO	0.0	0.0	0.0	0.0	
PP	2.0	1.1	0.0	0.0	
TOT	1.9	0.6	2.7	0.9	
SIX SEX RELATED BUI					
FO	1.5	0.6	1.9	0.7	
AN	0.0	0.0	120.0	0	
RT	1.6	1.1	0.0	0.0	
CC	0.0	0.0	0.0	0.0	
PU	0.0	0.0	120.8	5	
CO	0.0	0.0	0.0	0.0	
PP	2.0	1.1	0.0	0.0	
TOT	1.9	0.6	2.7	0.9	
SIX SEX RELATED BUI					
FO	1.5	0.6	1.9	0.7	
AN	0.0	0.0	120.0	0	
RT	1.6	1.1	0.0	0.0	
CC	0.0	0.0	0.0	0.0	
PU	0.0	0.0	120.8	5	
CO	0.0	0.0	0.0	0.0	
PP	2.0	1.1	0.0	0.0	
TOT	1.9	0.6	2.7	0.9	
SIX SEX RELATED BUI					
FO	1.5	0.6	1.9	0.7	
AN	0.0	0.0	120.0	0	
RT	1.6	1.1	0.0	0.0	
CC	0.0	0.0	0.0	0.0	
PU	0.0	0.0	120.8	5	
CO	0.0	0.0	0.0	0.0	
PP	2.0	1.1	0.0	0.0	
TOT	1.9	0.6	2.7	0.9	
SIX SEX RELATED BUI					
FO	1.5	0.6	1.9	0.7	
AN	0.0	0.0	120.0	0	
RT	1.6	1.1	0.0	0.0	
CC	0.0	0.0	0.0	0.0	
PU	0.0	0.0	120.8	5	
CO	0.0	0.0	0.0	0.0	
PP	2.0	1.1	0.0	0.0	
TOT	1.9	0.6	2.7	0.9	
SIX SEX RELATED BUI					
FO	1.5	0.6	1.9	0.7	
AN	0.0	0.0	120.0	0	
RT	1.6	1.1	0.0	0.0	
CC	0.0	0.0	0.0	0.0	
PU	0.0	0.0	120.8	5	
CO	0.0	0.0	0.0	0.0	
PP	2.0	1.1	0.0	0.0	
TOT	1.9	0.6	2.7	0.9	
SIX SEX RELATED BUI					
FO	1.5	0.6	1.9	0.7	
AN	0.0	0.0	120.0	0	
RT	1.6	1.1	0.0	0.0	
CC	0.0	0.0	0.0	0.0	
PU	0.0	0.0	120.8	5	
CO	0.0	0.0	0.0	0.0	
PP	2.0	1.1	0.0	0.0	
TOT	1.9	0.6	2.7	0.9	
SIX SEX RELATED BUI					
FO	1.5	0.6	1.9	0.7	
AN	0.0	0.0	120.0	0	
RT	1.6	1.1	0.0	0.0	
CC	0.0	0.0	0.0	0.0	
PU	0.0	0.0	120.8	5	
CO	0.0	0.0	0.0	0.0	
PP	2.0	1.1	0.0	0.0	
TOT	1.9	0.6	2.7	0.9	
SIX SEX RELATED BUI					
FO	1.5	0.6	1.9	0.7	
AN	0.0	0.0	120.0	0	
RT	1.6	1.1	0.0	0.0	
CC	0.0	0.0	0.0	0.0	
PU	0.0	0.0	120.8	5	
CO	0.0	0.0	0.0	0.0	
PP	2.0	1.1	0.0	0.0	
TOT	1.9	0.6	2.7	0.9	
SIX SEX RELATED BUI					
FO	1.5	0.6	1.9	0.7	
AN	0.0	0.0	120.0	0	
RT	1.6	1.1	0.0	0.0	
CC	0.0	0.0	0.0	0.0	
PU	0.0	0.0	120.8	5	
CO	0.0	0.0	0.0	0.0	
PP	2.0	1.1	0.0	0.0	
TOT	1.9	0.6	2.7	0.9	
SIX SEX RELATED BUI					
FO	1.5	0.6	1.9	0.7	
AN	0.0	0.0	120.0	0	
RT	1.6	1.1	0.0	0.0	
CC	0.0	0.0	0.0	0.0	
PU	0.0	0.0	120.8	5	
CO	0.0	0.0	0.0	0.0	
PP	2.0	1.1	0.0	0.0	
TOT	1.9	0.6	2.7	0.9	
SIX SEX RELATED BUI					
FO	1.5	0.6	1.9	0.7	
AN	0.0	0.0	120.0	0	
RT	1.6	1.1	0.0	0.0	
CC	0.0	0.0	0.0	0.0	
PU	0.0	0.0	120.8	5	
CO	0.0	0.0	0.0	0.0	
PP	2.0	1.1	0.0	0.0	
TOT	1.9	0.6	2.7	0.9	
SIX SEX RELATED BUI					
FO	1.5	0.6	1.9	0.7	
AN	0.0	0.0	120.0	0	
RT	1.6	1.1	0.0	0.0	
CC	0.0	0.0	0.0	0.0	
PU	0.0	0.0	120.8	5	
CO	0.0	0.0	0.0	0.0	
PP	2.0	1.1	0.0	0.0	
TOT	1.9	0.6	2.7	0.9	
SIX SEX RELATED BUI					
FO	1.5	0.6	1.9	0.7	
AN	0.0	0.0	120.0	0	
RT	1.6	1.1	0.0	0.0	
CC	0.0	0.0	0.0	0.0	
PU	0.0				

SAT SOCIAL ATTENTION

	TR1	TR2
AT	32.8 ± 3.2	30.6 ± 3.1
SA	4.9 ± 2.1	105.8 ± 3.3
AF	24.1 ± 3.0	22.0 ± 2.1
TU	2.8 ± 4.4	100.5 ± 3.3
TOT	60.3 ± 5.4	56.7 ± 3.2
	101.0	M= 1.0

HSG NON-SOCIAL

TR1 TR2

SC	2.3 ± 1.8	1.1 ± .4
SR	3.9 ± 2.2	105.0 ± .1
SH	0.0 ± 0.0	0.0 ± 0.0
JP	0.0 ± 0.0	128.0 ± 0.0
EA	1.2 ± 1.2	0.0 ± 0.0
DK	1.3 ± .9	109.2 ± 6
SI	0.0 ± 0.0	0.0 ± 0.0
SU	2.2 ± .4	1.0 ± .4
SAP	0.0 ± 0.0	67.3 ± .2
PO	0.0 ± 0.0	104.0 ± .1
EO	1.1 ± 1.1	2.1 ± .1
SC	38.2 ± 3.7	50.5 ± 4.4
DI	5.4 ± 4.0	101.0 ± 1.3
EX	44.9 ± 7.7	47.2 ± 6.4
LV	.9 ± .2	106.0 ± .1
WA	11.6 ± 2.1	9.0 ± 1.6
FP	0.0 ± 0.0	0.0 ± 0.0
DP	0.0 ± 0.0	0.0 ± 0.0
L5	1.1 ± .1	2.6 ± .1
A3	0.0 ± 0.0	0.0 ± 0.0
A6	0.0 ± 0.0	0.0 ± 0.0
A5	0.0 ± 0.0	0.0 ± 0.0
TOT	103.8 ± 9.0	113.7 ± 6.1
	90.0	M= 2.1

SOCIO SOCIAL CONTACT

	TR1	TR2
1R	15.2 ± 3.4	15.3 ± 3.3
MO	7.6 ± 3.2	4.2 ± 1.4
GR	3.9 ± 3.3	111.3 ± .3
SH	4.9 ± 1.2	2.4 ± .7
TOT	28.2 ± 7.4	22.1 ± 4.9
	117.0	M= .2

SEX SEX-RELATED BEH

	TR1	TR2
PO	2.0 ± .8	2.8 ± .7
AM	0.0 ± 0.0	0.0 ± 0.0
MT	2.2 ± .2	128.0 ± 0.0
GO	0.0 ± 0.0	0.0 ± 0.0
PU	1.1 ± .1	128.0 ± .1
CO	0.0 ± 0.0	0.0 ± 0.0
PF	0.0 ± 0.0	2.2 ± .2
TOT	2.3 ± .6	3.1 ± .7
	107.5	M= .9

OFF OFFENSE

	TR1	TR2
TH	5.2 ± .7	9.1 ± 1.2
AK	3.7 ± 1.8	45.0 ± 5
BT	42.1 ± 4.0	26.0 ± 4.2
CH	2.7 ± .6	45.0 ± 5
AG	3.4 ± .1	117.3 ± 2
TOT	53.9 ± 4.5	39.1 ± 4.3
	62.0 ± 5	M= 6.2 ± 5

OFF OFFENSE ANTI-VALANCE

	TR1	TR2
OB	20.9 ± 2.0	27.4 ± 2.9
OU	4.8 ± .8	78.5 ± 1.3
PF	9.6 ± 1.7	17.3 ± 2.3
SP	8.0 ± 0.0	128.0 ± 0.0
TOT	35.4 ± 2.9	30.8 ± 5.2
	69.5 ± 5	M= 6.9 ± 5

DIA DISTANCE ANTI-VALANCE

	TR1	TR2
22	4.7 ± 2.2	10.0 ± 2.5
CI	7.9 ± 2.0	5.6 ± 1.0
UR	8.3 ± 1.9	103.3 ± 1.9
BA	5.4 ± 1.2	13.3 ± 2.3
TOT	30.3 ± 4.7	37.7 ± 4.5
	94.0	M= 1.3

DIA DEFENSIVE ANTI-VALANCE

	TR1	TR2
OR	0.0 ± 0.0	4.4 ± .3
UP	0.0 ± 0.0	104.0 ± .0
DU	0.0 ± 0.0	0.0 ± 0.0
DS	0.0 ± 0.0	0.0 ± 0.0
TOT	0.0 ± 0.0	108.4 ± 0.0
	102.0	M= 2.4

ARF ARRESTED FLIGHT

	TR1	TR2
CR	2.1 ± 2.0	0.0 ± 0.0
FR	27.4 ± 5.0	20.7 ± 3.8
EK	0.0 ± 0.0	100.0 ± 0.0
SL	0.0 ± 0.0	0.0 ± 0.0
TOT	27.9 ± 5.0	20.7 ± 3.8
	99.0	M= 1.2

ESC ESCAPE

	TR1	TR2
FC	3.4 ± .3	0.0 ± 0.0
KV	0.0 ± 0.0	128.0 ± 0.0
RT	16.4 ± 1.6	16.2 ± 1.7
FL	0.0 ± 0.0	0.0 ± 0.0
OM	3.4 ± .2	112.0 ± 0.0
TOT	17.4 ± 1.6	16.2 ± 1.7
	113.0	M= 1.2

EXPERIMENT : VUSPCA

2

TREATMENT 3 (TR1) : CONTROL

17

TREATMENT 2 (TR2) : VISAVIS-DEF

NUMBER OF ENCOUNTERS : 17

NONE

FREQ

MED NON-SOCIAL

TR1

TR2

SC 1.1+ .4 135.0

SR .6+ .2 135.0

SH .1+ .1 135.0

JP 1.1+ .7 100.0

EA 0.0+ 0.0 110.5

DK .1+ .1 135.0

SI 0.0+ 0.0 100.0

SU 1.5+ .3 134.5

SAP .3+ .1 71.5

PD .3+ .2 0.0+ 0.0

KD .2+ .2 119.0

SC 26.8+ 2.5 23.2+ 3.0

DI .6+ .4 110.5

ER 26.1+ 2.8 21.1 3.1

LV .5+ .2 .3+ .1

VA 4.9+ .7 132.5

AM 0.0+ 0.0 100.0

PF 0.0+ 0.0 100.0

DF 0.0+ 0.0 100.0

LS .3+ .3 134.5

A3 .1+ .1 134.5

A4 0.0+ 0.0 100.0

A5 0.0+ 0.0 100.0

TOT 64.1+ 6.8 64.4+ 6.3

136.0

M= 1

SOCIAL CONTACT

TR1

TR2

IM 35.0+ 2.9 20.0+ 3.0

MO 7.0+ 1.3 19.7+ 2.0

CR 1.6+ .4 7.8+ .9

SM 4.4+ .9 4.9+ 1.1

TOT 28.0+ 5.4 37.4+ 6.0

119.5

M= .7

SEX SEX-RELATED BEN

TR1

TR2

PD 3.0+ 1.6 6.3+ 1.6

AM 0.0+ 0.0 97.3

RT 0.0+ 0.0 0.0+ 0.0

GC 0.0+ 0.0 0.0+ 0.0

PU 0.0+ 0.0 137.5

CO 0.0+ 0.0 0.0+ 0.0

PF .2+ .1 136.2

TOT 6.1+ 1.6 6.8+ 1.6

94.0

M= 3.1

DPA OFFENSIVE AMBIVALENCE

TR1

TR2

OS 31.1+ 3.5 24.0+ 3.9

OU 8.8+ 1.5 103.0

PY 17.4+ 2.4 14.4+ 2.1

SF 0.0+ 0.0 0.0+ 0.0

TOT 57.3+ 6.9 41.6+ 6.2

102.5

M= 2.1

DIA DISTANCE AMBIVALENCE

TR1

TR2

ZE 8.5+ 1.8 3.2+ .8

CI 5.6+ .9 105.5

UR 6.9+ 1.2 4.2+ 1.1

BA 1.9+ .5 137.5

TOT 22.9+ 2.9 16.6+ 2.3

83.0

M= 4.2

ARF ARRESTED FLIGHT

TR1

TR2

CR .6+ .4 119.5

FR 14.0+ 2.1 10.9+ 1.9

KK 0.0+ 0.0 0.0+ 0.0

SL 0.0+ 0.0 0.0+ 0.0

TOT 14.6+ 2.0 11.0+ 1.9

102.5

M= 2.1

ESC ESCAPE

TR1

TR2

FC .1+ .1 136.0

EV 2+ 2 163.5

FL 17.6+ 1.6 12.4+ 1.2

RL 0.0+ 0.0 0.0+ 0.0

ON .3+ .3 177.0

TOT 18.1+ 1.1 13.8+ 1.1

82.0

M= 4.3

DIA DEFENSIVE AMBIVALENCE

TR1

TR2

OB .1+ .1 136.0

UP .1+ .1 136.0

DU 0.0+ 0.0 0.0+ 0.0

DS 0.0+ 0.0 0.0+ 0.0

TOT 1+ 1 136.0

M= 2

SAT SOCIAL ATTENTION

	TR1	TR2
AT	24.4+ 3.6	26.4+ 3.8
SA	1.3+ .3	1.2+ .4
AP	23.4+ 3.0	21.8+ 2.3
TU	2.7+ .4	2.2+ .3
TOT	51.8+ 5.3	50.3+ 5.1

134.0 M= .1

SOCIAL CONTACT

	TR1	TR2
EM	32.0+ 8.2	40.3+ 4.1
MO	10.7+ 2.4	14.4+ 3.4
CR	3.3+ 1.0	7.2+ 2.8
SM	6.8+ 1.6	9.9+ 2.4
TOT	52.9+ 12.1	71.7+ 12.5

112.0 M= 1.3

SEX SEX-RELATED EDH

	TR1	TR2
FO	5.3+ 3.2	4.3+ 1.5
AM	0.0+ 0.0	9.0+ 0.0
MT	0.0+ 0.0	0.0+ 0.0
CC	0.0+ 0.0	0.0+ 0.0
PJ	0.0+ 0.0	14.2+ 1.1
CD	0.0+ 0.0	127.5+ 1.1
PP	3+ .1	144.2+ 1.1

134.0 M= .2

TOT 5.4+ 3.2 4.8+ 1.6 M= 2.8 #

HOME DURATION

MSO NON-SOCIAL

	TR1	TR2
SC	2.4+ 1.1	1.4+ .9
SR	3+ .2	137.0+ .6
SH	0+ .0	133.5+ .2
JP	1.1+ .6	176.0+ 0.0
EA	0.0+ 0.0	131.0+ .4
DK	0+ .0	138.0+ .4
SE	0.0+ 0.0	14.3+ .1
SU	1.3+ .3	14.5+ .7
SAP	3+ .1	54.0+ .7
PD	5+ .3	68.5+ .7
ED	2+ .2	119.0+ .1
SC	51.7+ 5.6	55.8+ 9.2
DI	8+ .5	127.0+ .1
EX	31.3+ 3.4	104.0+ 4.2
LV	3+ .1	124.1+ .1
VA	7.7+ 1.3	137.3+ 4.4
FP	0.0+ 0.0	134.5+ .0
DP	0.0+ 0.0	144.5+ .0
LS	1.8+ 1.8	144.5+ .9
A3	1.3+ .1	124.7+ .7
AA	0.0+ 0.0	100.0+ .0
AA	0.0+ 0.0	144.5+ .0
AA	0.0+ 0.0	144.5+ .0

112.0 M= 1.3

TOT 104.7+ 4.1 121.8+ 13.1

OFF OFFENSE

	TR1	TR2
TH	4.2+ 1.7	4.2+ 1.4
AE	1.0+ .3	141.5+ .4
AT	14.2+ 4.9	13.2+ 2.7
CH	2.7+ 1.0	101.3+ .8
AC	1.1+ .5	139.3+ .6
TOT	35.0+ 5.8	25.8+ 4.2

113.0 M= 1.2

OPA OFFENSIVE AMBIVALENCE

	TR1	TR2
OE	19.2+ 2.3	16.4+ 2.4
OU	5.0+ .9	117.5+ .5
PT	14.1+ 1.9	13.8+ 2.1
SP	0.0+ 0.0	144.5+ .0
TOT	38.2+ 4.6	32.3+ 4.5

111.0 M= 1.3

DIA DISTANCE AMBIVALENCE

	TR1	TR2
ZE	10.4+ 2.8	4.0+ 1.0
CI	7.7+ 1.7	5.0+ 1.4
OM	7.1+ 1.3	6.1+ 1.6
BA	1.4+ .4	120.0+ .9
TOT	27.1+ 4.1	17.8+ 3.4

101.0 M= 2.2

DIA DEFENSIVE AMBIVALENCE

	TR1	TR2
OK	.0+ .0	.2+ .1
UP	.0+ .0	133.0+ .2
DU	0.0+ 0.0	0.0+ 0.0
DS	0.0+ 0.0	0.0+ 0.0
TOT	.0+ .0	.3+ .2

133.0 M= .4

AIR ARRESTED FLIGHT

	TR1	TR2
CR	1.8+ 1.3	170.3+ .5
FR	16.3+ 3.2	15.4+ 3.0
EK	0.0+ 0.0	129.5+ .0
SL	0.0+ 0.0	0.0+ 0.0
TOT	20.4+ 3.0	15.1+ 3.0

113.0 M= 1.2

ESC ESCAPE

	TR1	TR2
FC	.3+ .3	.3+ .3
EV	.3+ .3	.2+ .2
RT	14.7+ 1.3	91.0+ 1.3
FL	0.0+ 0.0	0.0+ 0.0
OM	3.7+ 4.3	74.0+ 2.0
TOT	21.0+ 4.1	16.2+ 2.2

109.5 M= 1.5

SUPERLIGHT : AAYAMCA

NUMBER OF TREATMENTS : 2

TREATMENT 1 (TR1) : CONTROL

NUMBER OF ENCOUNTERS : 6

TREATMENT 2 (TR2) : ACQUA-VIS-VIS-DEP

NUMBER OF ENCOUNTERS : 6

HOME FREQUENCY

NSO NON-SOCIAL

	TR1	TR2
SC	9+ .4 1.3+ .4	M= .4
SR	3+ .2 2+ .3+ .2	M= .7
SH	1+ .1 32.0	M= 0.0
JP	3+ .2 20.0+ 0.0	M= .4
EA	1+ .1 1+ .1	M= 0.0
DK	6+ .3 32.0	M= .1
SI	1+ .1 1.0+ 0.0+ 0.0	M= .1
SU	2.0+ .6 22.0	M= 1.0
SAP	1.0+ .3 11.1+ .9	M= 1.2
PD	3+ .3 0.0	M= 11.6
SD	4+ .3 21.1+ .1	M= 1.4
SC	30.4+ 4.8 33.3+ 5.0	M= 2.1
DI	6+ .6 24.0	M= 1.7
EX	16.1+ 4.4 49.4+ 3.8	M= 2.1
LV	4.6+ .7 11.0	M= 4.9
WA	2.4+ .5 5.3+ 1.0	M= 11.0
PP	0.0+ 0.0 0.0+ 0.0	M= 4.6
DP	0.0+ 0.0 22.0	M= 0.0
LS	1.0+ .4 7.1+ 1.1	M= 1.0
AJ	5+ .5 3+ .3	M= 11.1
AS	1+ .1 28.0	M= .2
A5	1+ .1 28.0	M= 1.0
A6	1+ .1 28.0	M= 1.0
TOT	82.1+ 9.6 112.0+ 9.1	M= 4.4

SAT SOCIAL ATTENTION

AT 28.6+ 2.5

TR1

TR2

M= 11.8

SA 12.9+ 1.4

TR1

TR2

M= 1.0

AP 12.9+ 1.4

TR1

TR2

M= 11.5

TU 4.3+ .8

TR1

TR2

M= 9.1

TOT 46.1+ 3.4

TR1

TR2

M= 11.4

SOC SOCIAL CONTACT

IN 10.3+ 2.6

TR1

TR2

M= 3.4

MO 4.6+ 1.5

TR1

TR2

M= 1.4

CR 3+ .2

TR1

TR2

M= .A

SW 2.3+ .7

TR1

TR2

M= .6

TOT 17.6+ 4.5

TR1

TR2

M= 2.2

SEX SEX-RELATED BEN

FO 3+ .5

TR1

TR2

M= 0

AM 3+ .2

TR1

TR2

M= .4

MT 1+ .1

TR1

TR2

M= 0

GG 0.0+ 0.0

TR1

TR2

M= 1.0

PU 3+ .3

TR1

TR2

M= 1.0

CO 0.0+ 0.0

TR1

TR2

M= 1.0

PP 3+ .2

TR1

TR2

M= .2

TOT 1.4+ .6

TR1

TR2

M= .1

OFF OFFENSE

TH 1.1+ .7

TR1

TR2

M= .6

AK 8+ .4

TR1

TR2

M= 1.5

BT 26.9+ 4.1

TR1

TR2

M= .2

CH 5.3+ 1.5

TR1

TR2

M= 3.1

AG 9+ .7

TR1

TR2

M= .1

TOT 34.9+ 5.0

TR1

TR2

M= 1.1

OFA OFFENSIVE ANTI-VEHICLE

OS 33.3+ 3.9

TR1

TR2

M= 6.9

OU 4.3+ 1.8

TR1

TR2

M= .2

PV 2.3+ 1.6

TR1

TR2

M= .1

SP 0.0+ 0.0

TR1

TR2

M= 0.0

TOT 40.3+ 6.8

TR1

TR2

M= 4.2

M= 4.2

DIA DEFENSIVE ANTI-VEHICLE

OB 1+ .1

TR1

TR2

M= 0.0

UP 0.0+ 0.0

TR1

TR2

M= 0.0

DU 1+ .1

TR1

TR2

M= 0.0

DS 0.0+ 0.0

TR1

TR2

M= 0.0

TOT 3+ .2

TR1

TR2

M= 0.0

AAT ABSTRACT FLIGHT

CR 3+ .2

TR1

TR2

M= 2.1

FR 19.9+ 3.6

TR1

TR2

M= 1

MX 0.0+ 0.0

TR1

TR2

M= 0.0

SL 0.0+ 0.0

TR1

TR2

M= 0.0

TOT 20.1+ 3.5

TR1

TR2

M= 3

M= 3

ESC ESCAPE

PG 0.0+ 0.0

TR1

TR2

M= 0.0

EV 0.0+ 0.0

TR1

TR2

M= 0.0

RT 16.8+ 1.8

TR1

TR2

M= 10.4

M= 10.4

FL 1+ .1

TR1

TR2

M= 1.0

OM 2.0+ .9

TR1

TR2

M= 0

TOT 18.8+ 1.7

TR1

TR2

M= 10.7

M= 10.7

SAT SOCIAL ATTENTION

	TR1	TR2
AT	35.2+ 5.6	35.2
EA	0.0+ 0.0	0.0
AP	18.8+ 3.3	2.3+ .8
TU	3.3+ 1.1	12.6+ 1.9
TOT	63.3+ 7.6	13.3+ 2.2

SDO SOCIAL CONTACT

	TR1	TR2
EM	15.9+ 5.2	7.3+ 2.3
RO	5.2+ 1.8	4.9+ 3.0
CR	2.9+ 1.1	2.9+ .5
SM	4.9+ 1.7	1.3+ .6
TOT	36.3+ 8.0	14.3+ 5.1

SEX SEX-RELATED BDN

	TR1	TR2
FO	.9+ .9	1.1+ .1
AK	.4+ .3	3.1+ .8
MT	.0+ .0	1.4+ .4
CU	0.0+ 0.0	3.1+ .5
PP	.2+ .2	0.0+ 0.0
CO	0.0+ 0.0	28.0+ .0
PP	.2+ .1	2.2+ .2
TOT	1.7+ .9	2.3+ .5

TOT 121.7+13.4 221.3+12.1
1.0 se M=10.6 se

OFF OFFENSE

	TR1	TR2
TH	1.2+ .7	9+ .3
AK	.7+ .4	23.5+ .2
BT	21.1+ 2.9	24.3+ 3.7
CH	2.6+ .7	24.5+ .6
AC	1.3+ 1.2	3+ .1
TOT	26.9+ 3.1	26.6+ 3.8

DFA OFFENSIVE ANTHILLAGE

	TR1	TR2
OS	22.0+ 5.9	12.4+ 1.5
OU	3.1+ 1.4	3.4+ 1.1
PV	3.7+ 2.9	1.3+ .4
SP	0.0+ 0.0	26.0+ .0
TOT	28.8+ 7.0	17.1+ 2.3

DIA DISTANCE ANTHILLAGE

	TR1	TR2
ZZ	2.2+ 1.1	1.7+ .3
CI	1.4+ .9	1.4+ 1.0
VR	20.2+ 3.6	12.0+ 3.7
BA	2.0+ .7	2.4+ 1.1
TOT	25.8+ 3.6	16.5+ 4.3

TOT 26.9+ 3.7 16.0+ 1.8
11.0 se M=6.9 se

DEA DEFENSIVE ANTHILLAGE

	TR1	TR2
OK	1+ .1	31.3+ .3
UP	0.0+ 0.0	37.0+ .0
DU	1+ .1	31.3+ .0
DS	0.0+ 0.0	0.0+ 0.0
TOT	2+ .1	32.0+ .3

ARF ARRESTED FLIGHT

	TR1	TR2
CR	.3+ .3	0.0+ 0.0
FR	32.0+ 9.3	30.3+ 8.0
RK	0.0+ 0.0	27.0+ .0
SL	0.0+ 0.0	20.0+ 0.0
TOT	32.3+ 9.4	30.3+ 8.0

ESC ESCAPE

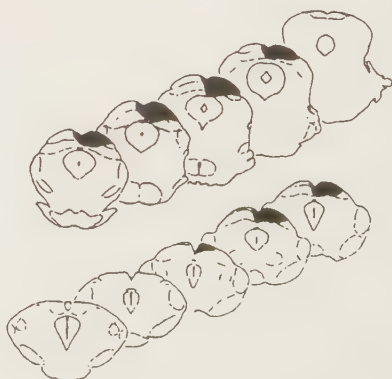
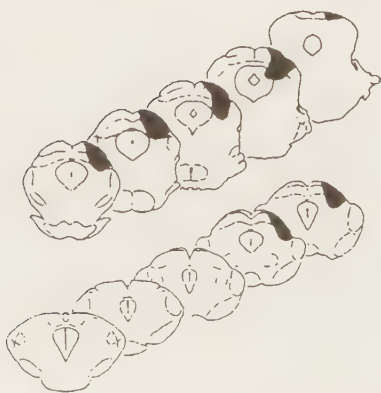
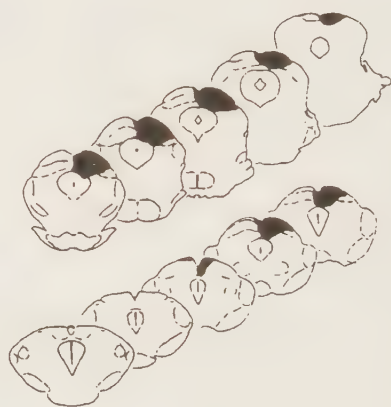
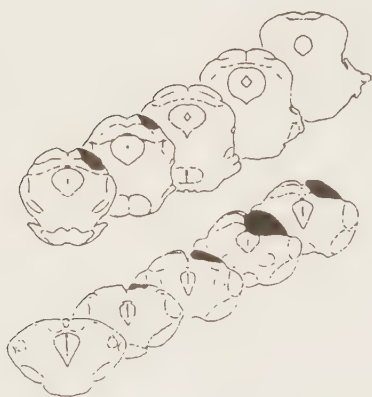
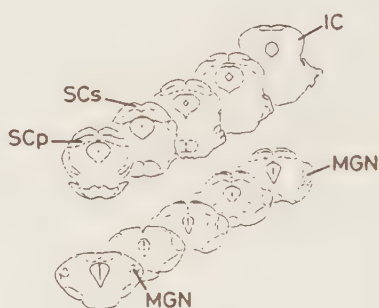
	TR1	TR2
FC	0.0+ 0.0	0.0+ 0.0
EV	0.0+ 0.0	0.0+ 0.0
RT	14.7+ 2.7	9.8+ 1.4
FL	.4+ .4	0.0+ 0.0
OM	2.9+ 3.5	31.0+ .0
TOT	26.9+ 3.7	16.0+ 1.8

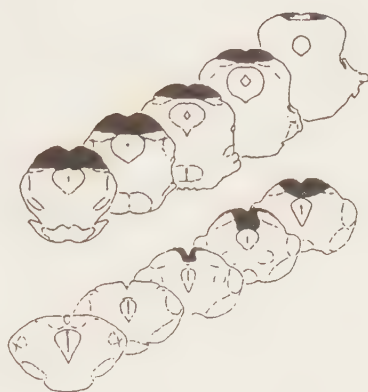
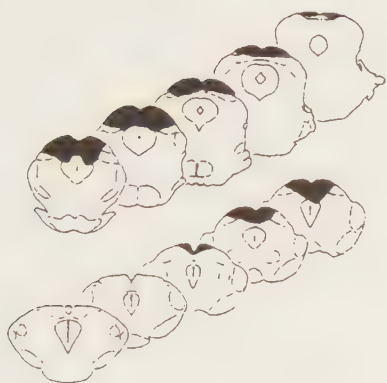
TOT 26.9+ 3.7 16.0+ 1.8
11.0 se M=6.9 se

2. Appendix B

Histological analysis of brain lesions as effected uni- and bilaterally in the superior colliculus SC, or in the medial geniculate nucleus MGN.

SCs=stratum superficiale of SC,
SCp=stratum profundum of SC,
IC=inferior colliculus (for location of sections see Fig. 5).

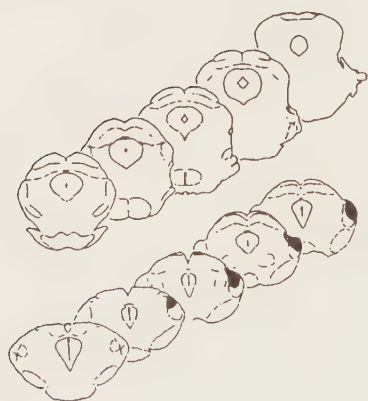
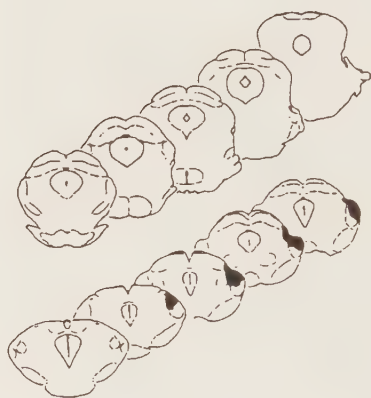
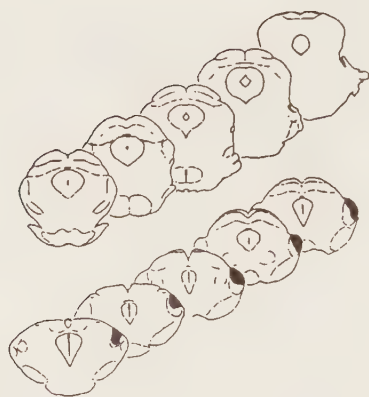




Unilateral lesions in the Superior Colliculus (p. 110)

Bilateral lesions in the Superior Colliculus (p. 111)

Unilateral lesions in the Medial Geniculate Nucleus (p.112)



VIII. LITERATURE

- Adrian, E.D. (1953) The mechanism of olfactory stimulation in the mammal. *Adv. Sci. Lond.* 9: 417-420.
- Alberts, J.R. (1974) Producing and interpreting experimental olfactory deficits. *Physiol. Behav.* 12: 657-670.
- Alberts, J.R. & Galef, B.G. (1971) Acute anosmia in the rat: A behavioural test of a peripherally-induced olfactory deficit. *Physiol. Behav.* 6: 619-621.
- Alberts, J.R. & Galef, B.G. (1973) Olfactory cues and movement: stimuli mediating intraspecific aggression in the wild norway rat. *J. comp. Physiol. Psychol.* 85/2: 233-242.
- Anderson, P.K. (1964) Lethal alleles in *mus musculus*: local distribution and evidence for isolation of demes. *Science* 145: 177-178.
- Anderson, P.K. & Hill, J.L. (1965) *Mus musculus*: Experimental induction of territory formation. *Science* 148: 1753-1755.
- Barlow, G.W. (1968) Ethological units of behaviour, in: *The central nervous system and fish behaviour*, ed. D. Ingle. pp. 217-232. University of Chicago Press. Chicago.
- Beach, F.A. (1942) Analysis of the stimuli adequate to elicit mating behaviour in the sexually inexperienced male rat. *J. comp. Psychol.* 33: 163-207.
- Benton, D. & Goldsmith, et al (1978) Adrenal activity in isolated mice and mice of different social status. *Physiol. Behav.* 20: 459-464.
- Berry, R.J. (1968) The ecology of an island population of the house mouse. *J. Anim. Ecol.* 37: 445-470.
- Bonnet, K.A. (1973) A method for the construction and use of contact occluders for small animals. *Physiol. Behav.* 10: 623-625.
- Bowers, J.M. & Alexander, B.K. (1967) Mice: Individual recognition by olfactory cues. *Science* 158: 1208-1210.
- Boxberger von, F. (1953) Vergleichende Untersuchungen ueber das visuelle Lernvermoege bei weissen Ratten und weissen Maeusen. *Z. Tierpsychol.* 9: 433-451.
- Boudreau, J.C. & Tsuchitani, C. (1968) Binaural interaction in the cat superior olive S-segment. *J. Neurophysiol.* 31: 143-213.
- Brain, P.F. (1974) What does individual housing mean to a mouse? *Life Sciences* 16: 187-200.
- Brain, P.F., et.al. (1982) Differentiating types of attack and defense in rodents, in: *Multidisciplinary approaches to aggression research*, eds. P.F. Brain & D. Benton. Elsevier, Holland.
- Brain, P.F., et.al. (1982a) Involvement of various senses in responses to individual housing in laboratory mice. 1. The olfactory sense.

- Boll. Zool. 49: 213-222.
- Brain, P.F., et.al. (1982b) Involvement of various senses in responses to individual housing in laboratory albino mice. 2. The tactile sense. Boll. Zool. 49: 223-227.
- Breipohl, W. et.al. (1985) Investigations of cell replacement in the olfactory epithelium. Neuroscience Letters, suppl. 19: S 7.
- Brown, G.E. & Remley, N.R. (1971) The effects of septal and olfactory bulb lesions on stimulus reactivity. Physiol. Behav. 6: 497-501.
- Bruce, H.M. (1959) An exteroceptive block to pregnancy in the mouse. Nature 184: 105.
- Busnel, R.G. & Fish, J.F. (1980) eds. Animal Sonar Systems. Plenum Press, New York.
- Bullock, T.H. (1983) Implications for neuroethology from comparative neurophysiology, in: Advances in vertebrate neuroethology, NATO ASI Series, Vol. 56, eds. J.P. Ewert, et.al. Plenum Press, New York and London. p. 53-76.
- Butler, R.A. (1975) The influence of the external and middle ear on auditory discriminations, in: Handbook of Sensory Physiology V.2. Auditory Systems, eds. M. Abeles, et.al. Springer Verlag, Berlin, Heidelberg, New York. p. 247-260.
- Cain, D.P. (1974) The role of the olfactory bulb in limbic mechanism. Psychol. Bull. 81/10: 654-671.
- Cairncross, K.D. et.al. (1975) Effect of amitriptyline on avoidance learning in rats following olfactory bulb ablation. Pharm. Biochem. Behav. 3: 1063-1067.
- Cairncross K.D. et.al. (1978) Olfactory projection system, drugs and behaviour: A review. Psychoneuroendocrinology 4: 253-272.
- Cairns, R.B. & al (1984) On fighting in mice: is there a sensitive period for isolation effects? Anim. Behav. 33/1: 166-180.
- Camhi, J.M. (1984) Neuroethology. Sinauer Associates Inc. Sunderland, Massachusetts.
- Catanzaro de, D. (1981) Facilitation of intermale aggression in mice through exposure to receptive females. J. comp. physiol. Psychol. 95/4: 638-645.
- Chance, M.R.A. (1962) An interpretation of some agonistic postures, the role of "cut-off" acts and postures. Proc. Zool. Soc. Lond. 8: 71-89.
- Clancy, A.N. et.al. (1984) Male hamster copulatory responses to a high molecular weight fraction of vaginal discharge: effects of vomeronasal organ removal. Physiol. Behav. 33: 653-660.
- Collett, T.S. (1983) Sensory guidance of motor behaviour, in: Animal Behaviour I. Causes and Effects, eds. T.R. Halliday & P.J.B. Sla-

- ter. Blackwell Scientific Publications.
- Cox, Th.P. (1984) Ethological isolation between local populations of house mice (*M. musculus*) based on olfaction. *Anim. Behav.* 32: 1068-1077.
- Crowcroft, P. (1955) Territoriality in wild house mice (*M. musculus*). *J. Mammalogy* 36: 299-301.
- Crowcroft, P. & Rowe, F.P. (1963) Social Organization and territorial behaviour in the wild house mouse (*M. musculus*). *Proc. Zool. Soc. London* 140: 517-531.
- Crowcroft, P. (1966) *Mice all over*. Dufour editions. GB.
- Dixon, A.K. (1982) A possible olfactory component in the effects of diazepam on social behaviour of mice. *Psychopharmacol.* 77: 246-252.
- Dixon, A.K. (1986) Ethological Aspects of Psychiatry. *Archives Suisses de Neurol. et de Psych.* 137/5: 151-163.
- Dixon, A.K. & Mackintosh, J.H. (1971) Effects of female urine upon the social behaviour of adult male mice. *Anim. Behav.* 19: 138-140.
- Dixon, A.K. & Mackintosh, J.H. (1975) The relationship between physiological condition of female mice and the effects of their urine on the social behaviour of adult males. *Anim. Behav.* 23: 513-520.
- Dixon, A.K. & Mackintosh, J.H. (1976) Olfactory mechanisms affording protection from attack to juvenile mice. *Z. Tierpsychol.* 41: 225-234.
- Douglas, R.J. et.al. (1969) Olfactory lesions, emotionality and activity. *Physiol. Behav.* 4: 379-381.
- Draeger, U.C. & Hubel, D.H. (1975) Responses to visual stimulation and relationship between visual, auditory and somatosensory inputs in mouse superior colliculus. *J. Neurophysiol.* 38: 690-713.
- Draeger, U.C. (1978) Observations on monocular deprivation in mice. *J. Neurophysiol.* 41/1: 28-42.
- Drickamer, L.C. (1986) Peripheral anosmia affects puberty- influencing chemosignals in mice: Donors and recipients. *Physiol. Behav.* 37: 741-746.
- Ehret, G. (1974) Age dependent hearing loss in normal hearing mice. *Naturwissenschaften* 61: 506-507.
- Ehret, G. (1976) Critical bands and filter characteristics in the ear of the house mouse (*M. musculus*). *Biol. Cybern.* 24: 35-42.
- Ehret, G. (1983) Peripheral anatomy and physiology II of the mouse auditory system, in: *The auditory psychobiology of the mouse*,

- ed. J.F. Willot. Charles C. Thomas, Publisher. Springfield, Illinois, USA. p. 169-200.
- Ehret, G. & Dreyer, A. (1984) Localization of tones and noise in the horizontal plane by unrestrained house mice (*M. musculus*). *J. exp. Biol.* 109: 163-174.
- Ehret, G. & Haack, B. (1982) Ultrasound recognition in house mice: Key-stimulus configuration and recognition mechanisms. *J. comp. Physiol.* 148: 245-251.
- Ehret, G. & Haack, B. (1984) Motivation and arousal influence on sound-induced maternal pup-retrieving behaviour in lactating house mice. *Z. Tierpsychol.* 65: 25-39.
- Etienne, A.S., et. al. (1985) Short distance homing in a small mammal: the role of exteroceptive cues and path integration. *Experientia* 41: 122-125.
- Ewert, J.P. (1976) *Neuro-Ethologie*. Heidelberger Taschenbuecher. Springer-Verlag, Berlin, Heidelberg, New York.
- Ewert, J.P. (1985) Concepts in vertebrate neuroethology. *Anim. Behav.* 33: 1-29.
- Ewert, J.P., Capranica, R.R. & Ingle, D.J. (1983) *Advances in vertebrate Neuroethology*. NATO ASI Series. Series A: Life Sciences, Vol. 56. Plenum Press. New York, London.
- Finlay, B.L. & Sengelaub, D.R. (1981) Toward a neuroethology of mammalian vision: ecology and anatomy of rodent visuomotor behaviour. *Beh. Brain Res.* 3/2: 133-149.
- Fries de, J.C. & McClearn, G.E. (1970) Social dominance and darwinian fitness in the laboratory mouse. *The Amer. Natural.* 104: 408-411.
- Gleeson, R.A. (1978) Functional adaptations in chemosensory systems. in: *Sensory ecology*. ed. M.A. Ali. pp 291-317. Plenum Press, New York.
- Goldberg, J.M. & Brown, P.B. (1969) Response of binaural neurons of dog superior olivary complex to dichotic tonal stimuli: Some physiological mechanisms of sound localization. *J. Neurophysiol.* 32: 613-636.
- Goodale, M.A., Foreman, N.P. & Milner, A.D. (1978) Visual orientation in the rat: A dissociation of deficits following cortical and collicular lesions. *Exp. Brain. Res.* 31: 445-457.
- Goodale, M.A. (1981) Visuomotor organization of pecking in the pigeon. in: *Advances in vertebrate neuroethology*, eds. J.P. Ewert, R.R. Capranica, D.J. Ingle. Series A: Life Sciences vol. 56. Plenum Press. New York and London. p. 349-358.
- Goyens, J. & Noirot, E. (1975) Effects of cohabitation with females on

- aggressive behaviour between male mice. *Develop. Psychobiol.* 8/1: 79-84.
- Grant, E.C. (1963) An analysis of the social behaviour of the male laboratory rat. *Behaviour* 21: 260-281.
- Grant, E.C. & Mackintosh, J.H. (1963) A comparison of the social postures of some common laboratory rodents. *Behaviour* 21: 246-259.
- Grant, E.C., Mackintosh, J.H. & Lerwill, C.J. (1970) The effect of a visual stimulus on the agonistic behaviour of the golden hamster. *Z. Tierpsychol.* 27: 73-77.
- Griffin, D.R. (1953) Bat sounds under natural conditions with evidence for the echolocation of insect prey. *J. exp. Zool.* 123: 435-466.
- Griffin, D.R. (1958) ed., *Listening in the dark*. Yale University Press, New Haven, Conn., USA.
- Griffin, D.R. et.al. (1960) The echolocation of flying insects by bats. *Anim. Behav.* 8: 141-154.
- Grobstein, P., et.al. (1985) Prey orienting in frogs: Accounting for variations in output with stimulus distance. *J. comp. Physiol. A*/156: 775-785.
- Guthrie, D.M. (1980) *Neuroethology*. Blackwell Scientific Publications.
- Gyger, M. & Schenk, F. (1983) Semiotical approach to the ultrasonic vocalization in the woodmouse (*Apodemus sylvaticus*). *Behaviour* 84: 244-257.
- Haack, B. & Markl, H. & Ehret, G. (1983) Sound communication between parents and offspring, in: *The auditory psychobiology of the mouse*, ed. J.F. Willot. Charles C. Thomas, Publisher. Springfield, Illinois, USA. p. 57-97.
- Harding, J.W. et.al. (1978) Denervation of the primary olfactory pathway in mice: II. Long-term effect of intranasal ZnSO₄ irrigation on behaviour, biochemistry and morphology. *Brain. Res.* 140: 271-285.
- Harrington, J.E. (1976) Recognition of territorial boundaries by olfactory cues in mice (*M. musculus L.*). *Z. Tierpsychol.* 41: 295-306.
- Harris, L.R., et. al. (1980) Integration of visual and auditory space in the mammalian superior colliculus. *Nature* 288: 56-59.
- Heiligenberg, W. (1984) Jamming avoidance in the electric fish, in: *Comparative physiology of sensory systems*, eds. L. Bolis et.al. Cambridge University Press, Cambridge. p. 490-492.
- Hildebrand, F.B. (1977) in: *A handbook of numerical and statistical techniques*, ed. J.H. Pollard. Cambridge University Press,

Cambridge. p. 28-29.

Hirsch, J.D. (1980) The neurochemical sequelae of olfactory bulbectomy. *Life Sciences* 26: 1551-1559.

Hoyle, G. (1984) The scope of neuroethology. *The Behavioural and Brain Sciences* 7: 367-412.

Huber, F. (1983) Implications of insect neuroethology for studies on vertebrates, in: *Advances in vertebrate neuroethology*, eds: J.P. Ewert, R.R. Capranica & D.J. Ingle. Plenum Press.

Huber, F. & Markl, H. (1983) *Neuroethology and behavioural physiology. Roots and growing points.* Springer-Verlag. New York, Heidelberg, Berlin.

Huerta, M.F. & Harting, J.K. (1984) The mammalian superior colliculus: Studies of its morphology and connections, in: *The comparative neurology of the optic tectum*, ed. H. Vanegas. Plenum Press, New York. p. 687-773.

Ingle, D.J. (1981a) Brain mechanisms of visual localization by frogs and toads, in: *Advances in vertebrate neuroethology*, eds. J.P. Ewert, R.R. Capranica, D.J. Ingle. Series A: *Life Sciences* vol. 56. Plenum Press. New York and London. p. 177-226.

Ingle, D.J. (1981b) New methods for analysis of vision in the gerbil. *Behavioural Brain. Res.* 3: 151-173.

Ingle, D.J. (1982) Organization of visuomotor behaviours in vertebrates, in: *Analysis of visual behaviour*, eds. D. Ingle et.al. Massachusetts Institute of Technology. p. 67-109.

Jay, M.F. & Sparks, D.L. (1984) Auditory receptive fields in primate superior colliculus shift with changes in eye position. *Nature* 309: 345-347.

Kalkowski, W. (1967) Olfactory bases of social orientation in the white mouse. *Folia Biol. Krakow* 15/1: 69-87.

Kalkowski, W. (1968a) Social orientation by traces in the white mouse. *Folia Biol. Krakow* 16/4: p. 307-322.

Kalkowski, W. (1968b) Visual control of social environment in the white mouse. *Folia Biol. Krakow* 16/3: 215-233.

Katz, R.J. (1976) Role of mystacial vibrissae in control of isolation induced aggression in mouse. *Behav. Biol.* 17: 399-403.

Keverne, E.B. (1978) Olfaction and taste - dual systems for sensory processing. *TINS* Aug.78: 32-34.

Knudsen, E.E. (1980) Sound Localization in Birds, in: *Comparative studies of hearing in Vertebrates*, eds: A.N. Popper & A.R. Fay. Springer Verlag, New York, Heidelberg, Berlin.

- Knudsen, E.E. & Konishi, M. (1979) Mechanisms of sound localization in the barn owl (*tyto alba*). J. comp. Physiol. 133: 13-21.
- Krsiak, M. (1976) Effect of Ethanol on aggression and timidity in mice. Psychopharmacol. 51: 75-80.
- Krsiak, M. & Janku, I. (1969) The development of aggressive behaviour in mice by isolation, in: Aggressive Behaviour, eds. S. Garattini & E.B. Sigg. Excerpta Medica Foundation, Amsterdam. p. 101-105.
- Lagerspetz, K. (1967) The effect of prior aggressive or sexual arousal on subsequent aggressive or sexual reaction in male mice. Scand. J. Psychol. 8: 1-9.
- Lagerspetz, K. & Portin, Z. (1968) Simulation of cues eliciting aggressive responses in mice at two age levels. The Journal of Genetic Psychology 113: 53-63.
- Lee van der, S. & Boot, L.M. (1955) Spontaneous pseudopregnancy in mice. Acta physiol. pharmac. neerl. 4: 442-443.
- Lehman, M.N. & Adams, D.B. (1977) A statistical and motivational analysis of the social behaviours of the male laboratory rat. Behaviour 61/3-4: 238-275.
- Lepri, J.J., et.al. (1985) Mouse vomeronasal organ: Effects on chemosignal production and maternal behaviour. Physiol. Behav. 35: 809-814.
- Luthardt, G. & Roth, G. (1983) The interaction of the visual and the olfactory systems in guiding prey catching behaviour in salamandra salamandra. Behaviour 83/1-2: 69-79.
- Mackintosh, J.H. (1970) Territory formation by laboratory mice. Anim. Behav. 18: 177-183.
- Mackintosh, J.H. (1973) Factors affecting the recognition of territory boundaries by mice. Anim. Behav. 21: 464-470.
- Mackintosh, J.H. (1978) The experimental analysis of overcrowding, in: Population control by social behaviour, eds. Ebling, F.J. & Stoddard, D.M. London: Institute of Biology, p. 157-180.
- Mackintosh, J.H. (1981) Behaviour of the house mouse, in: Biology of the House Mouse, ed. R.J. Berry. Zoological Society of London symposium 47. Academic Press, London, p. 337-365.
- Mackintosh, J.H., Chance, M.R.A. & Silverman, A.P. (1977) The contribution of ethological techniques to the study of drug effects, in: Handbook of Psychopharmacology Vol. 7, eds. L.L. Iverson, S.D. Iverson, S.H. Snyder.

- Mackintosh, J.H. & Grant, E.C. (1966) The effect of olfactory stimuli on the agonistic behaviour of laboratory mice. *Z. Tierpsychol.* 23: 584-587.
- Markl, H. & Ehret, G. (1973) Die Hoerschwelle der Maus (*Mus musculus*). *Z. Tierpsychol.* 33: 274-286.
- Marks, H.E., et.al. (1971) Effects of bilateral lesions of the olfactory bulbs of rats on measures of learning and motivation. *Physiol. Behav.* 7: 1-6.
- Masters, W.M. et.al. (1985) Sonar tracking of horizontally moving targets by the big brown bat *ptesicus fuscus*. *Science* 228: 1331-1333.
- Masterton, B. & Imig, T.I. (1984) Neural mechanisms for sound localization. *Ann. Rev. Physiol.* 46: 275-287.
- Matulionis, D.H. (1975) Ultrastructural study of mouse olfactory epithelium following destruction by $ZnSO_4$ and its subsequent regeneration. *Am. J. Anat.* 142: 67-90.
- Matulionis, D.H. (1976) Light-electron microscopic study of the degeneration and early regeneration of olfactory epithelium in the mouse. *Am. J. Anat.* 145: 79-100.
- McFarland, D.J. (1971) Feedback mechanisms in animal behaviour. Academic Press, London, New York.
- Meredith, M.A. & Stein, B.E. (1983) Interactions among converging sensory inputs in the superior colliculus. *Science* 221: 389-391.
- Mlinar, E.J. & Goodale, M.A. (1984) Cortical and tectal control of visual orientation in the gerbil: Evidence for parallel channels. *Exp. Brain. Res.* 55: 33-48.
- Morris, R. (1984) Developments of a water-maze procedure for studying spatial learning in the rat. *J. Neurosci. Methods* 11/1: 47-60.
- Mozell, M.M. & Hornung, D.E. (1984) Initial events influencing olfactory analysis, in: *Comparative Physiology of sensory systems*, eds. L. Bolis et.al. Cambridge University Press, Cambridge. p. 227-244.
- Mugford, R.A. & Nowell, N.W. (1970) Pheromones and their effect on aggression in mice. *Nature* 226: 967.
- Newsome, A.E. (1982) Homing by wild mouse mice displaced with or without the opportunity to see. *Austl. Wildl. Res.* 9: 421-426.
- Noirot, E. (1966) Ultra-sounds in young rodents, I. Changes with age in albino mice. *Anim. Behav.* 14: 459-462.
- Noirot, E. (1972) Ultrasounds and maternal behaviour in small rodents. *Dev. Psychobiol.* 5: 371-387.

- Novotny, M. et. al. (1985) Synthetic pheromones that promote inter-male aggression in mice. *Proc. Natl. Acad. Sci. USA* 82: 2059-2061.
- Nyby, J. & Whitney, G. (1978) Social status and ultrasonic vocalizations of male mice. *Behav. Biol.* 18: 285-289.
- Palmer, A.R. & King, A.J. (1982) The representation of auditory space in the mammalian superior colliculus. *Nature* 299: 248-249.
- Payne, R.S. (1971) Acoustic location of prey by barn owls (*Tyto alba*). *J. exp. Bio.* 54: 535-573.
- Payne, R.S. & Drury, W.H. (1958) *Tyto alba*, Part II. *Nat. Hist., N.Y.* 67: 316-323.
- Poeppel, E. (1973) Comment on "Visual System's View of Acoustic Space". *Nature* 243: 231.
- Poole, T.B. & Morgan, H.D.R. (1973) Differences in aggressive behaviour between male mice (*M. musculus*) in colonies of different sizes. *Anim. Behav.* 21: 788-795.
- Poole, T.B. & Morgan H.D.R. (1976) Social and territorial behaviour of laboratory mice (*M. musculus*) in small complex areas. *Anim. Behav.* 24: 476-480.
- Popper A.N. & Fay, R.R. (1980) Comparative studies of hearing in vertebrates. Springer-Verlag, New York, Berlin, Heidelberg.
- Powers, J.B. & Winans, S.S. (1975) Vomeronasal organ: Critical role in mediating sexual behaviour of the male hamster. *Science* 187: 961-963.
- Priestnall, R. (1973) The effects of litter size and postweaning isolation or grouping on adult emotionality in C3H mice. *Develop. Psychobiol.* 6: 217-244.
- Rehn, B., et.al. (1982) Effect of N-MIFM on the vomeronasal neuro-epithelium of mice. *Cell. Tiss. Res.* 225: 465-468.
- Rehn, B. et.al. (1982) Morphologische Veraenderungen am Riech-epithel von Maeusen nach olfactorischer Blockade mit N-methyl-formimino-Methylester. *Verh. Dtsch. Zool. Ges.* p. 227.
- Reimer, J.D. & Petras, M.L. (1967) Breeding structure of the house mouse *M. musculus* in a population cage. *J. Mammalogy* 48: 88-99.
- Roeder, K.D. (1963) Nerve cells and insect behaviour. Harvard University Press, Cambridge, Massachusetts.
- Ropartz, Ph. (1968a) Etude du determinisme olfactif de l'effet de groupe chez la souris male. *Rev. Comportement Anim.* 2/4: p.

35-78.

- Ropartz, Ph. (1968b) The relation between olfactory stimulation and aggressive behaviour in mice. *Anim. Behav.* 16: 97-100.
- Sachs, L. (1974) *Angewandte Statistik, Planung und Auswertung, Methoden und Modellle*. Springer-Verlag, Berlin, Heidelberg, New York.
- Sahibzada, N. et. al. (1986) Movements resembling orientation or avoidance elicited by electrical stimulation of the superior colliculus in rats. *J. Neurosci.* 6/3: 723-733.
- Saito, T.R. & Moltz, H. (1986) Copulatory behaviour of sexually naive and sexually experienced male rats following removal of the vomeronasal organ. *Physiol. Behav.* 37: 507-510.
- Sales, G.D. & Pye, J.D. (1974) *Ultrasonic communication by animals*. Chapman and Hall, London.
- Saunders, C.J. & Garfinkle, T.J. (1983) Peripheral anatomy and physiology of the mouse auditory system, in: *The auditory psychobiology of the mouse*, ed. J.F. Willot. Charles C. Thomas, Publisher, Springfield, Illinois, USA. p. 131-168.
- Scalia, F. & Winans, S.S. (1975) The differential projections of the olfactory bulb and accessory olfactory bulb in mammals. *J. Comp. Neur.* 161: 31-56.
- Schneider, G.E. (1969) Two visual systems. Brain mechanisms for localization and discrimination are dissociated by tectal and cortical lesions. *Science* 163: 895-902.
- Schuijf, A. & Hawkins, A.D. (1976) *Sound reception in fish*. Elsevier, Amsterdam.
- Scott, J.P. & Fredericson, E. (1951) The causes of fighting in mice and rats. *Physiol. Zool.* 24/4: 273-309.
- Shepherd, G.M. (1985) The olfactory system: the uses of neural space for a non-spatial modality, in: *Progress in Clinical and Biological research*, vol. 176, eds. M.J. Correia and A.A. Perachio. Alan R. Liss, p. 99-114.
- Shnerson, A. & Pujol, R. (1983) Development: Anatomy, electrophysiology and behaviour, in: *The auditory psychobiology of the mouse*, ed. J.F. Willot. C.C. Thomas, Publisher, Springfield, Illinois. p. 395-425.
- Sieck, M.H. (1972) The role of the olfactory system in avoidance learning and activity. *Physiol. Behav.* 8: 705-710.
- Sieck, M.H. & Baumbach, H.D. (1974) Differential effects of peripheral and central anosmia producing techniques on spontaneous behaviour patterns. *Physiol. Behav.* 13: 407-425.
- Siegel, S. (1956) *Nonparametric statistics for the behavioural sciences*.

ces. McGraw-Hill.

- Singer, A.G. et.al. (1984) Chemical studies of hamster vaginal discharge: Male behavioural responses to a high molecular weight fraction require physical contact. *Physiol. Behav.* 33: 645-651.
- Slotnik, B.M. & Leonard, C.M. (1975) A stereotaxic atlas of the albino mouse forebrain. U.S. Department of Health, Education and Welfare, Public Health Service, Rockville, Maryland, USA.
- Smith, C.G. (1938) Changes in the olfactory mucosa and the olfactory nerves following intranasal treatment with one per cent zinc sulfate. *Canadian Medical Association Journal* 39: 138-140.
- Smith, D.J. (1982) A device for the electrolytic decalcification of bone. *J. Histotech.* 5/4: 163-164.
- Snell, G.D. (1941) Biology of the laboratory mouse. Dover Publications, Inc., New York.
- Spallanzani, L. (1932) Opere di L. Spallanzani (1794-1798), 5 vols. Milano: Ulrico Hoepli.
- Stein, B.E. et.al. (1976) Relationship between visual and tactile representations in cat SC. *J. Neurophysiol.* 39: 401-419.
- Stiebler, I. & Ehret, G. (1985) Inferior colliculus of the house mouse. I. A quantitative study of tonotopic organization, frequency representation and tone-threshold distribution. *J. comp. Neurol.* 238: 65-76.
- Strasser, S. & Dixon, A.K. (1986) Effects of visual and acoustic deprivation on agonistic behaviour of the albino mouse (*M. musculus L.*). *Physiol. Behav.* 36: 773-778.
- Takagi, S.F. (1981) Multiple olfactory pathways in mammals: a review. *Chemical Senses* 6/4: 329-333.
- Thurlow, W.R. & Runge, P.S. (1967) Effect of induced head movements on localization of direction of sounds. *J. acoust. Soc. Amer.* 42/2: 480-488.
- Thinus-Blanc, C. (1978) Données comportementales sur la discrimination visuelle chez l'animal. *Année psychol.* 75: 457-491.
- Thor, D.H. & Ghiselly, W.B. (1975) Vibrissal anesthesia and suppression of irritable fighting in rats: a temporary duration of effect in experienced fighters. *Physiol. Psychol.* 3: 1-3.
- Tinbergen, N. (1951) The study of instinct. Oxford University Press.
- Uhrich, J. (1938) The social hierarchy in albino mice. *J. comp. Psychol.* 25: 373-413.
- Valzelli, L. (1969) Aggressive behaviour induced by isolation, in: *Aggressive Behaviour*, eds. S. Garattini & E.B. Sigg. Excerpta

- Medica Foundation, Amsterdam. p. 70-76.
- Valzelli, L. (1973) The "isolation-syndrome" in mice. *Psychopharmacologia* (Berlin) 31: 305-320.
- Wallach, H. (1940) The role of head movements and vestibular and visual cues in sound localization. *J. exptl. Psychol.* 27/4: 339-368.
- Walls, G.L. (1963) The vertebrate eye and its adaptive radiation. Hafner Publishing Company, New York.
- Wenzel, B.M. & Salzman, A. (1968) Olfactory bulb ablation or nerve section and pigeons' behaviour in non-olfactory learning. *Expl. Neurol.* 22: 472-479.
- Whitney, G. & Nyby, J. (1983) Sound communication among adults, in: *The auditory psychobiology of the mouse*, ed. J.F. Willot. C.C. Thomas, Springfield, Illinois. p. 98-129.
- Whitten, W.K. (1956) Modification of the oestrous cycle of the mouse by external stimuli associated with the male. *J. Endocrin.* 13: 399-404.
- Willard, F.H. & Ryugo, D.K. (1983) Anatomy of the central auditory system of the mouse, in: *The auditory psychobiology of the mouse*, ed. J.F. Willot. Charles C. Thomas, Publisher. Springfield, Illinois, USA. p. 201-304.
- Willot, J.F. (1983) ed. *The auditory psychobiology of the mouse*. Charles C. Thomas, Publisher. Springfield, Illinois, USA. p. 305-338.
- Wilson, J.P. (1966) Psychoacoustics of obstacle detection using ambient or self-generated noise. In: *Animal Sonar Systems, Biology and Bionics*, edited by R.G. Busnel. Jouey-en-Josas, France:INRA-CNRZ vol. I: 89-114.
- Wise, L.Z. & Irvine, R.F. (1983) Auditory response properties of neurons in deep layers of cat superior colliculus. *J. Neurophysiol.* 49/3: 674-685.
- Woolsey, T.A. & Van der Loos, H. (1970) The structural organization of layer IV in the somatosensory region (SI) of the mouse cerebral cortex: the description of a cortical field composed of discrete cytoarchitectonic units. *Brain. Res.* 17: 205-242.
- Wong, D. (1984) Spatial tuning of auditory neurons in the superior colliculus of the echolocating bat, *myotis lucifugus*. *Hearing Research* 16: 261-270.
- Yerkes, R.M. (1907) *The dancing mouse*. Macmillan, New York.

CURRICULUM VITAE

Stephan Strasser

30. April 1957	Geboren in Steckborn, als 2. der 3 Kinder von Emilie Maria und Werner Friedrich Strasser- Hagenbuechli.
1964-1970	Primarschule in Steckborn.
1970-1972	Sekundarschule in Steckborn.
1972-1976	Kantonsschule in Frauenfeld, Matura Typ C.
1976-1981	Biologiestudium mit Hauptfach Zoologie an der Universitaet Zuerich, Phil. Fakultaet II. Diplomarbeit: "Die Rolle der dorsalen Randregion des Bienenauges (<i>Apis mellifera</i>) bei der Kompassorientierung nach dem Himmelspolarisationsmuster" unter der Leitung von Prof. Dr. R. Wehner.
1984-1987	Dissertation am Sandoz Forschungsinstitut Bern AG (Industriestipendium der SANDOZ AG): "Neuroethology of Mouse Agonistic Behaviour" unter der Leitung von Prof. Dr. R. Wehner (Universitaet Zuerich) und Dr. A.K. Dixon (Sandoz Forschungsinstitut Bern AG).

Dozenten, deren Vorlesungen, Uebungen oder Praktika besucht wurden:

R. Bachofen, G. Baechli, E. Batschelet, Th. Baumann, G. Baumgartner, A. Binder, M. Birnstiel, H.R. Bossard, B. Briegel, E. Brun, H. Burla, P.S. Chen, Ph. Christen, C.D.K. Cook, A. Duebendorfer, E. Dubler, W. Egger, P. Endress, C.H. Eugster, J.R. Guenter, K. Hanselmann, H. Heimgartner, H.R. Hohl, Th. Honegger, R. Humbel, E. Jungen-Hauschtek, J. Kaegi, E. Kubli, H. Kummer, W. Kuendig, Th. Labhart, I. Mendoza-Heuer, G. Mindek, R. Noethiger, H.R. Oswald, R. Parish, R. Portmann, D. Rast, H. Rieber, R. Roessel, H.P. Ruffner, H. Schaeppi, P. Schmid, V. Schmid, K. Schneider, M.V. Srinivasan, I.D. Tacier, P. Tardent, K. Theiler, H. Wanner, R. Wehner, Ch. Weissmann, V. Wiemken, V. Ziswiler.

